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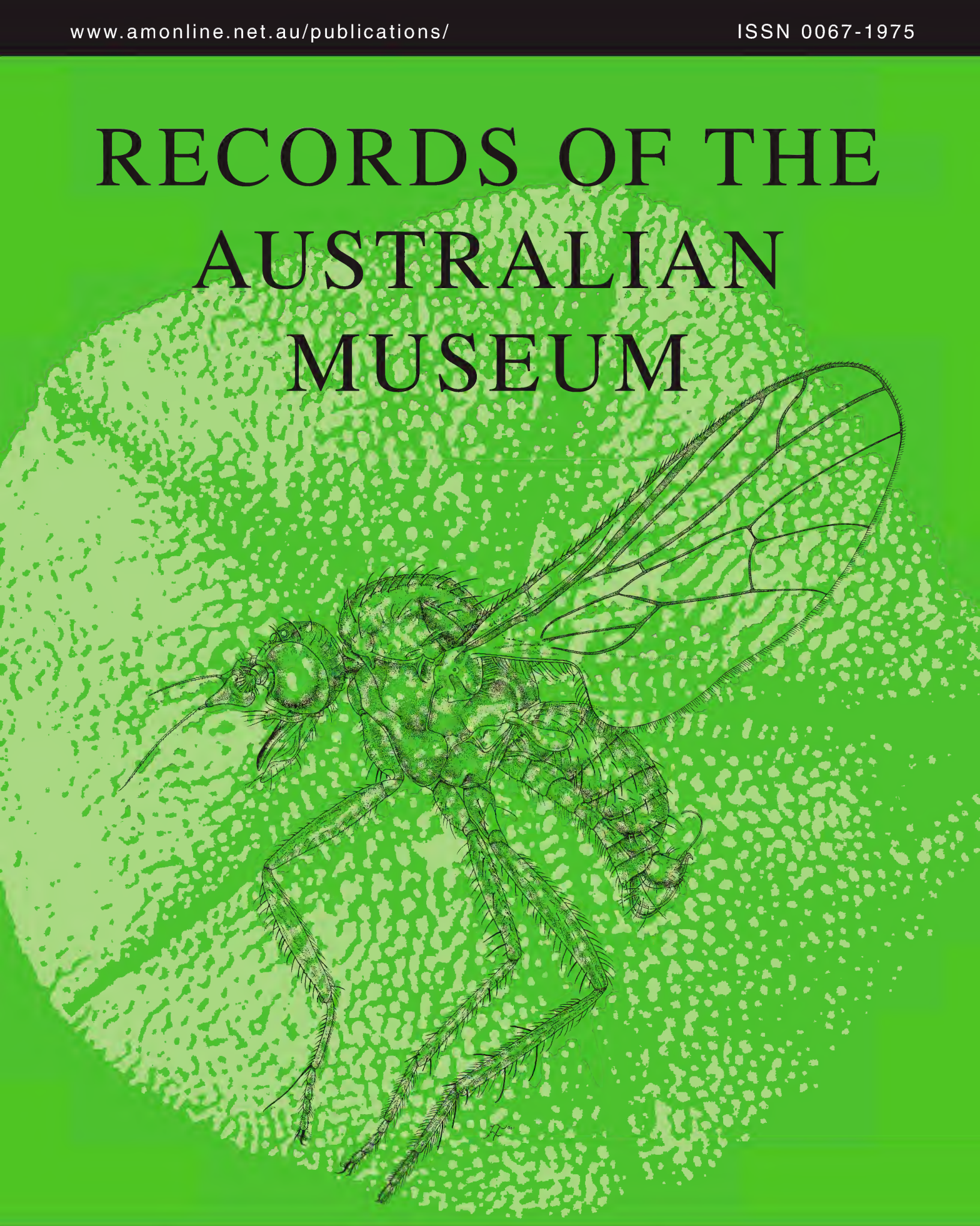
RECORDS OF THE AUSTRALIAN MUSEUM



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RECORDS OF THE AUSTRALIAN MUSEUM

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The **cover image**, by Hannah Finlay, is of a new empidid fly genus discovered by Australian Museum entomologist Dan Bickel*. These flies are primarily collected at light traps in tropical monsoonal woodlands of Cape York Peninsula—males are distinctive in having swollen antennae and a strong dorsoapical seta on their foreleg (see cover image). Hundreds of new species of animals are being described annually in *Records of the Australian Museum*, the results of important discoveries in anthropology, archaeolohgy and geology are also featured. Since 1999 the primary scientific literature published in print by the Australian Museum has also been freely available online at our website (in addition, certain earlier papers, are being scanned and uploaded). These and many other works may be purchased as bound issues from the Australian Museum Shop.

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The background image is the echinoderm *Asterodiscides elegans,* a species reported in waters off northeastern Australia (Rowe, 1977, *Records of the Australian Museum* 31[5]).

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Eusyllinae (Polychaeta: Syllidae) from Australia with the Description of a New Genus and Fifteen New Species

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ABSTRACT. Large collections of Syllidae (Polychaeta) from around Australia, housed at the Australian Museum (Sydney), have been examined and identified. Australian material from the Hamburgische Zoologische Museum der Universität, Hamburg, Germany was also examined. All known Australian species of the subfamily Eusyllinae (Syllidae) are described and figured. Some were examined using the Scanning Electron Microscope to illustrate characters and methods of reproduction in this subfamily. Keys to genera and species are given. A total of 53 species are reported from Australia belonging to 14 genera: *Amblyosyllis* Grube, 1857 (3 species); *Anoplosyllis* Claparède, 1868 (1 species); *Astreptosyllis* Kudenov & Dorsey, 1982 (2 species); *Eusyllis* Malmgren, 1867 (3 species); *Nudisyllis* Knox & Cameron, 1970 (1 species); *Odontosyllis* Claparède, 1863 (9 species); *Opisthodonta* Langerhans, 1879 (3 species); *Paraehlersia* San Martín, 2003 (2 species); *Paraopisthosyllis* Hartmann-Schröder, 1991 (4 species); *Pionosyllis* Malmgren, 1867 (15 species); *Psammosyllis* Westheide, 1990 (1 species); *Streptodonta* n.gen. (1 species); *Streptosyllis* Webster & Benedict, 1884 (3 species); and *Syllides* Örsted, 1845 (5 species). A total of 15 new species are described: *Amblyosyllis enigmatica, A. multidenticulata, Odontosyllis marombibooral; Opisthodonta hanneloreae, Paraopisthosyllis alternocirra, P. ornaticirra, Syllides tam, Pionosyllis rousei, P. kalimna, P. yolandae, P. mariae, P. mayteae, P. ancori, P. koolalya*, and *P. heterochaetosa*. A new name, *Pionosyllis hartmannschroederae*, is proposed for *Typosyllis (Langerhansia) longisetosa* Hartmann-Schröder, 1990 as this is junior homonym of *Pionosyllis longisetosa* (Hartmann-Schröder, 1965).

Additionally, five species are new records for Australia: *Odontosyllis gravelyi* Fauvel, 1930; *Opisthodonta morena* Langerhans, 1879; *Pionosyllis corallicola* Ding & Westheide, 1997; *Streptodonta pterochaeta* (Southern, 1914) and *Syllides japonicus* Imajima, 1966. A discussion of the reproduction and systematics of the subfamily is given.

SAN MARTÍN, GUILLERMO, & PAT HUTCHINGS, 2006. Eusyllinae (Polychaeta: Syllidae) from Australia with the description of a new genus and fifteen new species. *Records of the Australian Museum* 58(3): 257–370.

This is the second contribution to the Australian Syllidae, based on the large collections housed in the Australian Museum from all around Australia, and revision of material collected and described by Hartmann-Schröder (1979–1991). The material examined was collected predominantly from southern Australia, and no material was examined from north of 14°S on either the west or east coast of Australia. This paper also summarises material already published by San Martín (2002, 2005) and San Martín & López (2003). A general introduction to the family Syllidae is given by

* author for correspondence

San Martín (2005) in his revision of the subfamily Exogoninae in Australian waters. In this paper, all species belonging to the subfamily Eusyllinae are described and figured, and keys for identification provided. Comments are given on the other genera of Eusyllinae not currently known from Australia. Subsequent papers will deal with the subfamilies Syllinae and Autolytinae.

The subfamily Eusyllinae was erected by Malaquin (1893), for the genera *Syllides* Örsted, 1845; *Opisthodonta* Langerhans, 1879; *Pionosyllis* Malmgren, 1867; *Eusyllis* Malmgren, 1867; *Odontosyllis* Claparède, 1863; and *Amblyosyllis* Grube, 1857. Subsequently, Fauvel (1923) included the genera *Fauvelia* Gravier, 1900 (now considered a doubtful genus), *Streptosyllis* Webster & Benedict, 1884; and *Parapionosyllis* Fauvel, 1923 (now considered as belonging to the Exogoninae). Later, San Martín (2003) re-erected *Anoplosyllis* Claparède, 1868, and erected *Neopetitia* and *Paraehlersia* and placed them in the subfamily. Other genera considered to belong to the subfamily are *Palposyllis* Hartmann-Schröder, 1977; *Miscellania* Martín, Alós & Sardá, 1990; *Dioplosyllis* Gidholm, 1962; *Paraopisthosyllis* Hartmann-Schröder, 1991 (although with some doubts, see below); *Astreptosyllis* Kudenov & Dorsey, 1982; and *Streptospinigera* Kudenov, 1983. The genus *Psammosyllis* Westheide, 1990, which was not assigned to a subfamily when erected, is herein considered to belong to the Eusyllinae. In this paper, we erect a new genus, *Streptodonta*. Other genera previously assigned to this subfamily include: *Irmula* Ehlers, 1913 (now transferred to Hesionidae); *Clavisyllis* Knox, 1957; *Lamellisyllis* Day, 1960 (both questionable members of this subfamily); and *Rhopalosyllis* Augener, 1913 (now assigned to the Syllinae). *Nudisyllis* Knox & Cameron, 1970 is redefined. Currently 14 of these genera are known to occur in Australia.

This subfamily is heterogeneous and probably should be divided into several monophyletic groups (Glasby, 1994; San Martín, 2003). Until a detailed analysis (currently in preparation by senior author) is completed, however, we prefer to use the traditional classification of Eusyllinae.

A consistent diagnosis of this subfamily is difficult to provide because of the variability of many of the characters. Like most syllids, they are dorsally arched, convex, ventrally flat or concave. Size range of the subfamily Eusyllinae varies from minute to more than 30 mm long, occupying a similar range of habitats to members of Exogoninae (see San Martín, 2005). They often are fragile and Museum collections rarely contain complete, well-preserved specimens necessary for detailed studies. Eusyllinae typically lack colour markings. The palps are fused, partially fused or free from each other, depending upon the genera. Even within a genus, the degree of fusion of palps varies. *Nudisyllis* was originally described as lacking antennae and dorsal cirri, but this was based on data obtained from examination of damaged specimens, intact specimens have 3 antennae and dorsal cirri, so all Eusyllinae have three antennae that are typically long, extending beyond palps. Four lensed eyes and sometimes two additional eyespots are present, although these may fade with time on preserved material. The peristomium has two pairs of tentacular cirri, usually long and slender, and may be modified dorsally to form an occipital flap. Nuchal organs consist of two dorsolateral, densely ciliated grooves between the prostomium and peristomium. The genus *Amblyosyllis* (as well as *Clavisyllis* and *Lamellisyllis*) is characterized by having a nuchal organ consisting of two nuchal lappets, which strongly resemble those found in the subfamily Autolytinae. The pharynx is straight, except in *Amblyosyllis*, typically with a conical tooth that is located on the anterior margin opening or behind the anterior rim, or in the middle or posterior part of the pharynx. Other genera (*Syllides, Anoplosyllis, Streptosyllis, Astreptosyllis, Streptospinigera*) lack a pharyngeal tooth. These latter genera resemble each other and perhaps should be removed from the subfamily. *Amblyosyllis* has a long, slender, coiled pharynx, with a trepan, lacks a tooth, and margins of the pharynx are ornamented with soft papillae. This genus together with *Clavisyllis* and *Lamellisyllis* may also need to be removed from the Eusyllinae, since they have nuchal lappets instead of ciliated grooves as nuchal organs.

Parapodia are uniramous, with dorsal and ventral cirri, although dorsal cirri may be absent on chaetiger 2. Dorsal cirri typically are long, filiform, smooth, not articulated, although in *Paraopisthosyllis* and some species of *Pionosyllis* all or some are club-shaped and other species of *Pionosyllis* has short, exogonid-like dorsal cirri, although anteriorly they are long and smooth. Members of the Eusyllinae reproduce by epigamy (Garwood, 1991; Franke, 1999; San Martín, 2003). The eyes enlarge (see Figs 38A, 22A), colour patterns if present become far more marked and long, capillary notochaetae develop on middle and posterior segments (Figs 36D, 45E, 71B), which presumably are used in swimming. Members of the subfamily Exogoninae also reproduce by epigamy, but they attach their eggs either dorsally by means of capillary notochaetae of females, or ventrally by attaching them to the nephridial pore (San Martín, 2005). Some members of the genus *Nudisyllis* have been shown to brood dorsally, and some members of *Syllides* and *Pionosyllis* breed ventrally, but other information is lacking. San Martín (2005) has shown the usefulness of reproductive characters in the Exogoninae that may also prove useful in the Eusyllinae when more genera have been examined for these characters.

Some species of syllids are restricted to small geographical areas, and many examples can be found within the Australian fauna, but others have apparently wide distributions, and are regarded as being "cosmopolitan" species. Although increasingly such so-called "cosmopolitan" species are being found to represent suites of sibling species (see Westheide, 1971; Westheide & Hass-Cordes, 2001). In some of these examples, species exhibit no morphological differences and molecular techniques must be used to separate the species. Westheide & Hass-Cordes (2001) have used such techniques on syllids and found it useful. In some cases upon careful examination of these so-called "cosmopolitan" species has revealed small but consistent morphological differences and we have therefore described them as separate species. In other cases, we have been unable to find any morphological differences and so tentatively accept that the Australian Eusyllinae fauna includes these widely distributed species.

Material and methods

The material examined was mainly from the collections in The Australian Museum (AM), and was collected by many people including: N. Coleman, G. Wilson, J.K. Lowry, R.T. Springthorpe, H.E. Stoddart, P.A. Hutchings, A. Murray, T.J. Ward, P.C. Young, A. Jones, and others. Australian

material from the Zoologisches Museum of Hamburg (HZM), collected and identified by Hartmann-Schröder, has been re-examined. The specimens are preserved in 70% ethanol after having been fixed in formalin. Examinations were made using a compound microscope with interference contrast optics (Nomarsky). Drawings were made using a camera lucida drawing tube. Scanning Electron Microscope observations and photographs were made in the SIDI (Servicio Interdepartamental de Investigación) of the Universidad Autónoma de Madrid, Spain and at the SEM unit at the Australian Museum.

Information about aboriginal words for the names of several new taxa was obtained from Endacott (1973).

Some structures, e.g., nuchal organs or eyespots, are difficult to see. They are described only when they were visible on the specimens, although their presence cannot be excluded and certainly some species lack eyespots.

Categories of sizes of specimens given in the text are: small (<5 mm in length), medium (5–10 mm in length) and large (>10 mm in length). In syllids, the length of chaetal blades within fascicle typically decreases from dorsal to ventral (dorsoventral gradation); and also the shape and length of the chaetae may vary along the body, and therefore all descriptions include this information.

A useful compilation of polychaete terms are provided by Glasby *et al.* (2000) and by San Martín (2005).

The Material examined section lists material in a clockwise direction around Australia.

The following abbreviations are used in the Material examined:

AM	The Australian Museum, Sydney, NSW, Australia
BMNH	The Natural History Museum, London, UK
HMZ	Zoologisches Museum of Hamburg, Germany
LACM	Los Angeles County Museum, Los Angeles, USA
MNHN	Museum national d'Histoire naturelle, Paris, France
MNCNM	Museo Nacional de Ciencias Naturales de Madrid, Spain
NFMN	Naturhistorisches Forschungsinstitut Museum für Naturkunde, Berlin, Germany
SMNH	Naturhistoriska Riksmuseet, Stockholm, Sweden
SMF	Senckenberg Museum, Frankfurt, Germany
USNM	National Museum of Natural History, Washington, D.C, USA
MPUW	Museum Przydnicze Uniwersytetu Wroclawskiego, Wroclaw, Poland

Key to genera of Eusyllinae recorded from Australia

1 Body, rough, densely papillated; with short, inflated antennae and dorsal cirri (Fig. 50A) ..... *Paraopisthosyllis*

—— Body elongated, smooth, without epidermal papillae; antennae and cirri not inflated (except in some species of *Pionosyllis*, with some cirri inflated) 2

2 Nuchal organs as lappets (Fig. 2C). Pharynx long, highly convoluted with trepan, without mid-dorsal pharyngeal tooth (Fig. 3A) ..... *Amblyosyllis*

—— Nuchal organs as two ciliated grooves between prostomium and peristomium. Pharynx straight, not convoluted 3

3 Pharynx unarmed 4

—— Pharynx armed with single tooth, and or pharyngeal denticles 7

4 Aciculae of some anterior parapodia with inflated tips (Fig. 82I) ..... *Streptosyllis*

—— Aciculae without inflated tips (Fig. 6E) 5

5 Dorsal cirri all smooth, more or less club-shaped (Fig. 6A) ..... *Anoplosyllis*

—— Dorsal cirri from chaetiger 3 distinctly articulated (Fig. 90A) 6

6 Dorsal simple chaetae with distinct, longitudinally striated, distal hood (Fig. 9C). Compound chaetae unidentate. Ventral cirri of posterior parapodia distinctly elongated ..... *Astreptosyllis*

—— Dorsal simple chaetae without hood, or if present, small and not striated. Compound chaetae bidentate. Ventral cirri not elongated ..... *Syllides*

7 Pharynx with incomplete trepan formed by few teeth, backwardly directed, without mid-dorsal tooth (Fig. 20A) ..... *Odontosyllis*

—— Pharynx with mid-dorsal tooth 8

8 Pharyngeal tooth surrounded by incomplete circle of small denticles, forwardly directed, forming incomplete trepan (Fig. 10C) ..... *Eusyllis*

—— Single pharyngeal tooth present, trepan absent 9

9 Blades of compound chaetae with tendon connecting proximal tooth with margin (Fig. 74D). Pharyngeal tooth located near anterior rim, on middle of pharynx or posteriorly in mid line (Fig. 74A) ..... *Pionosyllis* (in part)

—— Blades of compound chaetae lacking such tendon 10

10 Pharyngeal tooth located far from anterior rim 11
—— Pharyngeal tooth located on, or close to anterior rim 14

11 Tentacular and some dorsal cirri inflated, club-shaped (Fig. 60A) ..... *Pionosyllis* (in part)
—— Without inflated dorsal cirri 12

12 Several anterior parapodia with distally inflated aciculae (Fig. 81A,C) ..... *Streptodonta* n.gen.
—— Without distally inflated aciculae 13

13 Palps free, not fused at base. Dorsal cirri long, slender, filiform, twice width of body. Ventral cirri of most anterior parapodia partially fused to parapodial lobes (Fig. 38E). Pharyngeal tooth located medially ..... *Opisthodonta*
—— Palps fused at bases and for most of their length. Dorsal cirri relatively short, about half width of body, ventral cirri not fused to parapodial lobes. Pharyngeal tooth located laterally (Fig. 80A) ..... *Psammosyllis*

14 Ventral cirri inserted medially or distally on parapodial lobes (Fig. 59B). Dorsal cirri of two lengths, long filiform and extremely short exogonid-like dorsal cirri that alternate along body (Fig. 59A) ..... *Pionosyllis* (in part)
—— Ventral cirri inserted at bases of parapodia. Dorsal cirri similar throughout or else differences between short and long cirri not as pronounced 15

15 Antennae, tentacular and anterior dorsal cirri articulated (adults) 16
—— Antennae and cirri smooth, sometimes rugose, pseudoarticulated 17

16 Segments posterior to proventricle fused in units of 2–3 segments (Fig. 78A). Subcirral papilla absent. Palps completely free ..... *Pionosyllis* (in part)
—— Segments not fused. Small subcirral papilla present on parapodia, shorter than width of dorsal cirrus (Fig. 44B). Palps fused at base ..... *Paraehlersia*

17 Dorsal cirri (except some anteriormost) exogonid-like, short, slightly longer than parapodial lobes (Fig. 56A) ..... *Pionosyllis* (in part)
—— Dorsal cirri long 18

18 Small to minute size (<5 mm in length). Pharynx short, shorter than proventricle, with a long tooth (Fig. 17A). Compound chaetae unidentate or provided with small, spine-like proximal tooth ..... *Nudisyllis*
—— Medium to large size (>5 mm in length). Pharynx long. Compound chaetae bidentate 19

19 Distinct prechaetal lobe present (Fig. 66B). Acicula straight, extending beyond parapodial lobes. Blades of compound chaetae without long, fine spines; without spiniger-like chaetae. Large size, distinctly macrofaunal (>10 mm in length) ..... *Pionosyllis* (in part)
—— Prechaetal lobe absent. Acicula distally knobbed, with 2 unequal lobes (Fig. 68J). Blades of compound chaetae with long, fine, distally ornamented spines (Fig. 63G); sometimes with spiniger-like chaetae (Fig. 63F). Medium size (>5 mm in length) ..... *Pionosyllis* (in part)

Genus *Amblyosyllis* Grube, 1857

Amblyosyllis Grube, 1857: 186.
Gattiola Johnston, 1865: 195.
Nicotia Costa, 1864: 160.
Pterosyllis Claparède, 1863: 46.
Thylaciphorus Quatrefages, 1865: 55.
Pseudosyllides Czerniavsky, 1882: 173.

Type species. *Amblyosyllis rhombeata* Grube, 1857 by monotypy.

Diagnosis. Body less than 5 mm in length, dorsoventrally flattened, extremely fragile, with few segments; peristomium and last segment without parapodia and chaetae, each with 2 pairs of cirri. Intersegmental constrictions strongly marked, midbody segments typically trapezoidal in shape. Prostomium with 3 antennae, 4 eyes, and usually 2 anterior eyespots, sometimes ventrally located. Palps short, less than length of prostomium, basally fused, divergent, usually ventrally folded, and difficult to see dorsally. Peristomium shorter than following segments, with 2 pairs

of tentacular cirri, and 2 nuchal organs, forming nuchal lappets, usually ciliated. Antennae, tentacular and dorsal cirri long, greater than body width, usually strongly coiled, sometimes forming skeins, smooth to indistinctly articulated, fragile. Pigmentary glands on dorsal and ventral cirri, sometimes forming distinct vesicles. Pharynx long, slender, highly convoluted, with trepan formed by several teeth, lacking median tooth. Proventricle proportionally small to body width. Ventral cirri large, located latero-posteriorly to parapodial lobes, similar in length. Compound chaetae, heterogomph, bidentate falcigers, numerous, present on all chaetigers, other types of chaetae rarely present; chaetae similar in all species. Pygidium with 2 long anal cirri, third length of dorsal cirri.

Remarks. Species belonging to this genus appear to be uncommon and are typically known from damaged incomplete specimens. Distinguishing species is therefore difficult. The structure of the nuchal organs and trepan are useful characters. The method of reproduction not well known, although a mature male has been observed with natatory chaetae and one species is known to brood eggs in a gelatinous mass, suggesting that the species of this genus are epigamic (Pernet, 1998).

Key to Australian species of *Amblyosyllis*

1 Nuchal lappets elongated, reaching middle of chaetiger 1 ..... *A. enigmatica* n.sp.

—— Nuchal lappets rounded, small, not extending beyond peristomium 2

2 Dorsal cirri with few, large, distinct vesicles (Fig. 5A). Compound chaetae with blades all similar, with small dorsoventral gradation in length (Fig. 5C). Trepan with monocuspid teeth ..... *A. vesiculosa*

—— Dorsal cirri with small, numerous granules (Fig. 3A). Compound chaetae with blades elongated (50–102 μm in length) (Fig. 3D), with distinct dorsoventral gradation in length. Trepan with 6 penta cuspid teeth, 2 of them separated by single monocuspid tooth ..... *A. multidenticulata* n.sp.

Amblyosyllis enigmatica n.sp.

Figs 1A–C, 2A–E

?*Amblyosyllis granosa*.—Augener, 1913: 243. Not Ehlers, 1897: 58.

Material examined. HOLOTYPE (AM W28943) AUSTRALIA: NEW SOUTH WALES: NW corner of Bowen Is., Jervis Bay, 35°06.81'S 150°46.11'E, dense bryozoan community under rock ledge, 13 m, coll. P. Serov & G.D.F. Wilson, 8 Dec 1993.

Additional material examined. Elizabeth Reef, Tasman Sea, 29°55.8'S 159°01.3'E, algae, reef flat, near wreck "Yoshin Maru Iwaki", 0.5 m, Elizabeth & Middleton Reefs Expedition, 1987, 14 Dec 1987, 6 + 3 on SEM stub (AM W28923).

Description. All specimens incomplete; holotype (Fig. 1A) mature, epigamic specimen, with regenerating posterior end, 3.5 mm long, 0.6 mm wide, with 10 chaetigers plus regenerating segments. Body large, segments trapezoidal (Fig. 2A), especially those of midbody, fragile; some specimens colourless, others strongly pigmented with 2–4 dorsal transverse dark bands on each segment, more marked on midbody. Prostomium oval, posteriorly notched, with 4 large red eyes in trapezoidal arrangement, covering lateral margins (Fig. 1A). Antennae long, inserted on anterior margin of prostomium, with distinct ceratophores (Fig. 2B). Palps free, fused basally, ventrally directed. Peristomium shorter than subsequent segments, with 2 pairs of tentacular cirri, dorsal ones twice as long as ventral; 2 ciliated, elongated nuchal lappets (Figs 1A, 2A–C), extending to middle of chaetiger 1, with dorsal, longitudinal row of pigment (Fig. 1A). Dorsal cirri long, as wide as body, indistinctly articulated, with numerous dark, granular inclusions, irregularly arranged in 3 longitudinal rows (Fig. 1A). Parapodial lobes long, conical, with long, digitiform prechaetal papilla (Fig. 2D). Ventral cirri conical, large, broad, arising ventrolaterally (Fig. 2D), upwardly directed, with granular, dark inclusions (Fig. 1A). Parapodia with 16–18 compound, heterogomph chaetae (Fig. 2E), blades distinctly bidentate; within fascicle blades exhibiting dorsoventral gradation in length (Fig. 1C), about 100 μm in length dorsally, 43 μm in length ventrally, with short spines on margin; about 6–8 aciculae per parapodium, straight, distally pointed. Pharynx slender, with several coils (Fig. 1A); trepan composed of 6 teeth each with 5 denticles (Fig. 1B). Proventricle extending through 1.5 segments, with 11–13 muscle cell rows. Holotype with notoacicula and capillary notochaetae, curved, digitiform, fleshy, dark structure arising from cirrophores from chaetiger 6 onwards (Fig. 1A, arrows); also, some ciliary bands present on lateral areas of first 4 chaetigers (Fig. 1A). Curved structure present on holotype missing on other material examined; function unknown.

Remarks. This species is characterized by having elongated nuchal lappets and a trepan with 6 teeth, each with 5 denticles; no species of the genus has been described with such a combination of characters. The general body form is almost identical to *Amblyosyllis granosa* Ehlers, 1897, from Magellan Strait and Galápagos Islands. Ehlers (1897) originally described this species with the anterior margin of the pharynx lacking teeth; subsequently, Westheide (1974) reported the same species from Galápagos, describing a trepan with 6 teeth, each formed by a long, median cusp and 2 lateral, much smaller ones. Examination of 1 specimen of the type series of *Amblyosyllis granosa* from Punta Arenas (Chile) (NFMN 5318) did not reveal any teeth on anterior margin of pharynx, as originally described, so, we are describing the Australian material as a new species *A. enigmatica*. A previous record of *A. granosa* from Australia by Augener (1913) is also referred with caution to *A. enigmatica* n.sp. Augener's material is not available for examination in the HZM and is presumed lost. *Amblyosyllis granosa*, however, could be present in Australian waters.

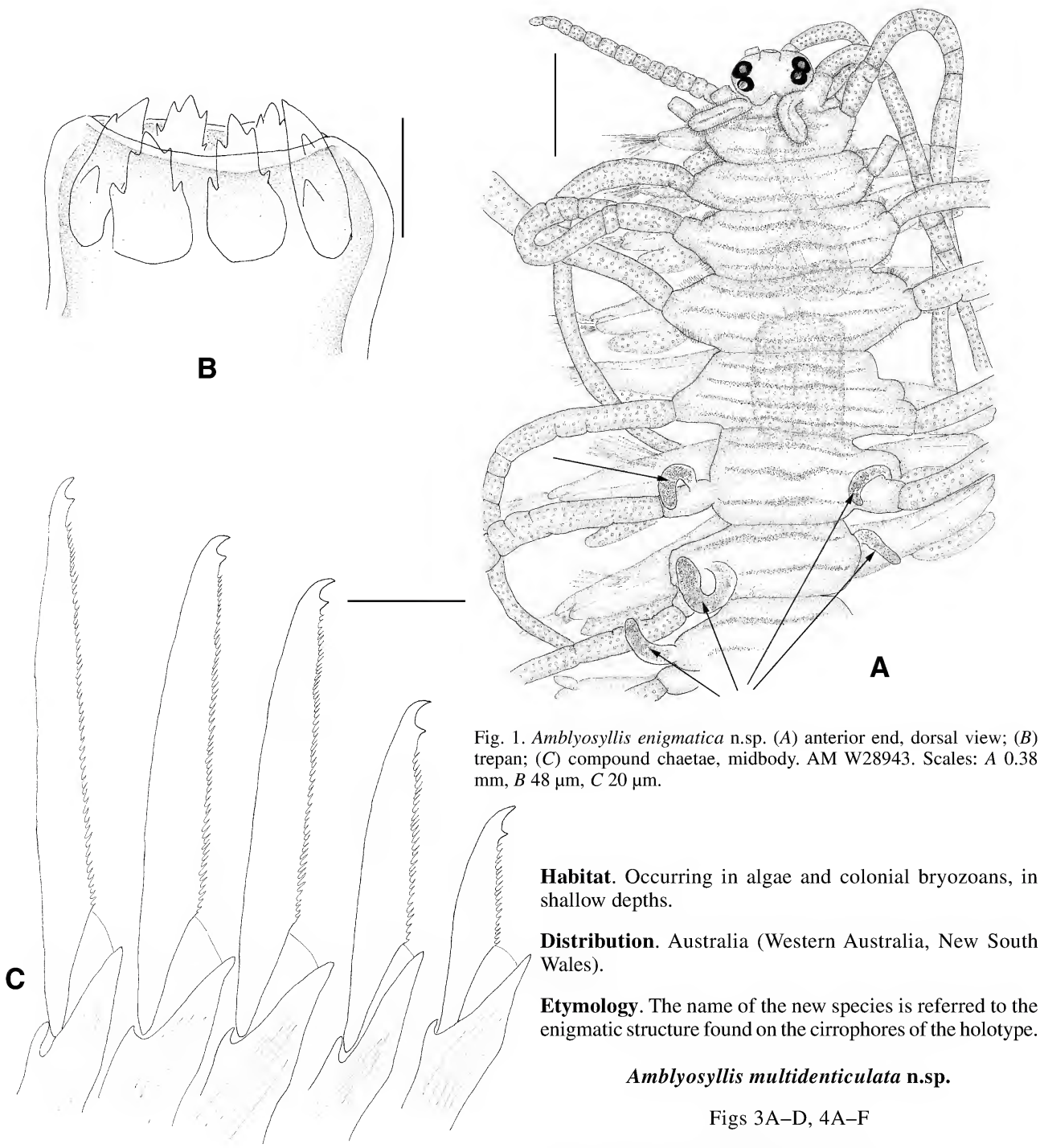


Fig. 1. *Amblyosyllis enigmatica* n.sp. (*A*) anterior end, dorsal view; (*B*) trepan; (*C*) compound chaetae, midbody. AM W28943. Scales: *A* 0.38 mm, *B* 48 µm, *C* 20 µm.

Habitat. Occurring in algae and colonial bryozoans, in shallow depths.

Distribution. Australia (Western Australia, New South Wales).

Etymology. The name of the new species is referred to the enigmatic structure found on the cirrophores of the holotype.

Amblyosyllis multidenticulata n.sp.

Figs 3A–D, 4A–F

Amblyosyllis spectabilis.—Haswell, 1920 (in part): 108, pl. 13, figs 4–10. Not Johnston, 1865: 195.

Material examined. HOLOTYPE (AM W502) AUSTRALIA: NEW SOUTH WALES: Port Jackson, 33°51'S 151°16'E, Feb 1920, coll. W.A. Haswell, mounted on microscope slide. PARATYPES NW corner of Bowen Is., Jervis Bay, 35°06.81'S 150°46.11'E, dense bryozoan community under rock ledge, 13 m, coll. P. Serov & G.D.F. Wilson, 8 Dec 1993, 3 on SEM stub (AM W26323); Halfway Reef, 200 m S of Sullivan Reef, Ulladulla, 35°21.42'S 150°29.31'E, red algae on rock ledges at base of wall, 13 m, coll. A. Murray, 3 May 1997, 2 (AM W28229); Port Jackson, 33°50'S 151°16'E, 1 (AM W25245), mounted on slide, id. W.A. Haswell as *A. spectabilis*.

Amblyosyllis formosa (Claparède, 1863) from European coasts is also similar to *A. enigmatica* n.sp., with regards to body form and the presence of long nuchal lappets; this species, however, has a trepan with 6 unidentate teeth (San Martín, 2003).

Little is known about reproduction within *Amblyosyllis*. The digitiform structures arising from cirrophores of chaetiger 6 onwards have never been described before, and their significance is unknown, but they may be used in reproduction, since they are only present on the single epigamic specimen examined. Knowing whether such structures occur in other species of the genus would be of interest.

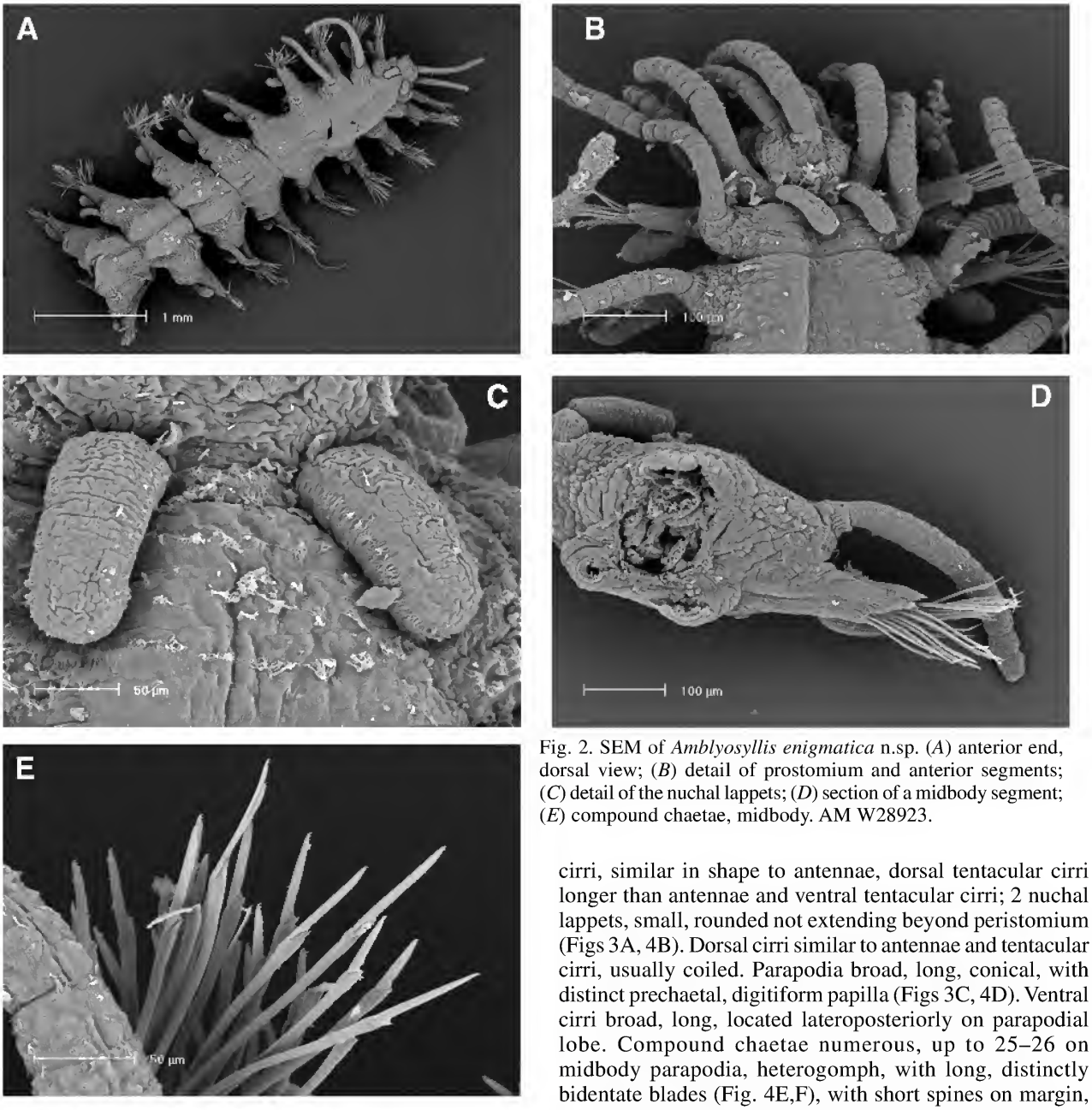


Fig. 2. SEM of *Amblyosyllis enigmatica* n.sp. (*A*) anterior end, dorsal view; (*B*) detail of prostomium and anterior segments; (*C*) detail of the nuchal lappets; (*D*) section of a midbody segment; (*E*) compound chaetae, midbody. AM W28923.

Description. Body compact (Fig. 4A), longest complete specimen examined 5.7 mm long, 0.6 mm wide, with 13 chaetigers and 1 posterior segment without parapodia or chaetae. Colour pattern variable; holotype collected in 1920 colourless. More recently collected paratypes with several dark, violet transverse dorsal bands of pigment on each segment; intensity of bands differs between individuals. Antennae, tentacular, dorsal and ventral cirri provided with numerous, dark, small globular glands (Fig. 3A). Prostomium wider than long, margins rounded, with 2 pairs of eyes in open trapezoidal arrangement (Fig. 3A), and 2 anterior, ventrally located, small eyespots. Antennae long, 3 times width of prostomium, distinctly articulated, with numerous articles, arising on anterior margin of prostomium from distinct ceratophores (Figs 3A, 4B). Palps ventrally directed (Fig. 4C), forming double lip over mouth, nearly invisible dorsally (Fig. 3A). Peristomium about half of length of subsequent segments, with 2 pairs of tentacular cirri, similar in shape to antennae, dorsal tentacular cirri longer than antennae and ventral tentacular cirri; 2 nuchal lappets, small, rounded not extending beyond peristomium (Figs 3A, 4B). Dorsal cirri similar to antennae and tentacular cirri, usually coiled. Parapodia broad, long, conical, with distinct prechaetal, digitiform papilla (Figs 3C, 4D). Ventral cirri broad, long, located lateroposteriorly on parapodial lobe. Compound chaetae numerous, up to 25–26 on midbody parapodia, heterogomph, with long, distinctly bidentate blades (Fig. 4E,F), with short spines on margin, and dorsoventral gradation in length of blades (Fig. 3D), length in midbody segments about 102 µm, 50 µm in length ventrally on midbody. Parapodia with 5–6 aciculae, straight, distally pointed. Pharynx long extending to chaetiger 5, narrow width, with several coils visible inside pharynx (Fig. 3A); trepan formed by 6 large teeth with 5 denticles separated by 1 unidentate, much smaller tooth (Fig. 3B). Proventricle small, located on chaetiger 5 (Fig. 3A), with 17–18 muscle cell rows. Pygidium small, trapezoidal, with 2 long anal cirri, half length of dorsal cirri.

Remarks. Haswell (1920) referred his Australian specimens to the European species *Amblyosyllis spectabilis* (Johnston, 1865), a poorly known species usually considered as a synonym of *A. formosa*, which may represent a suite of sibling species. Johnston's description of *Gattiola spectabilis* states that the pharynx is short and barrel shaped without teeth and long nuchal lappets are illustrated. In contrast, Haswell (1920) reported that teeth were present

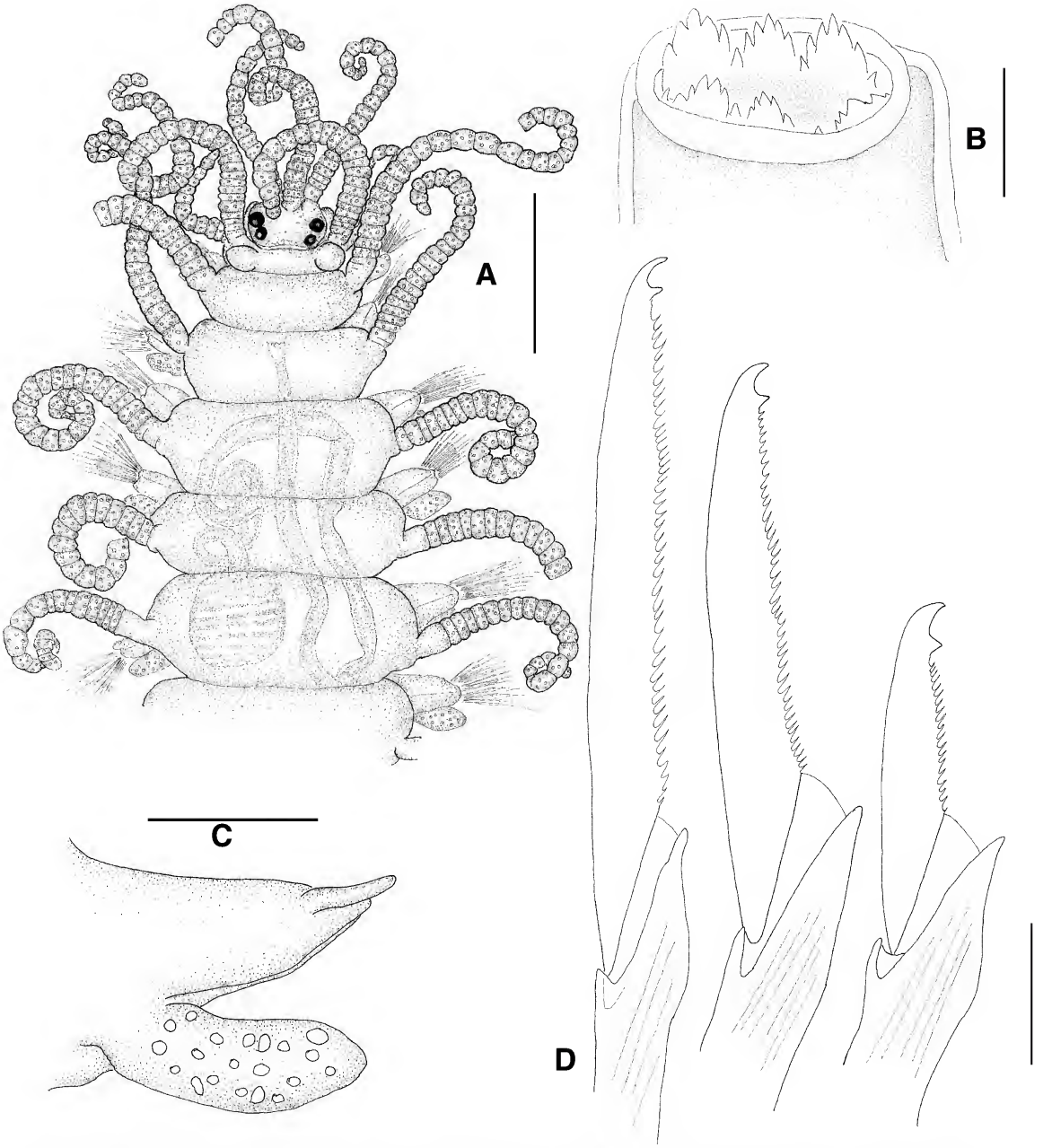


Fig. 3. *Amblyosyllis multidenticulata* n.sp. (*A*) anterior end, dorsal view; (*B*) trepan; (*C*) parapodial lobe and ventral cirrus; (*D*) compound chaetae, midbody. *A*: AM W502 (holotype); *B,C*: AM W28229 (paratypes); *D*: AM W26323 (paratypes). Scales: *A* 0.38 mm, *B* 48 µm, *C* 0.18 mm, *D* 20 µm.

in the pharynx. Re-examination of this material has shown that it belongs to a new species, *Amblyosyllis multidenticulata*. This new species is characterized by having small nuchal lappets and a trepan comprising 6 teeth each with 5 denticles, which are each separated by 1 small tooth (Fig. 3B); no other described species of this genus has been described with this arrangement of teeth on the trepan. The most similar species is *Amblyosyllis madeirensis* Langerhans, 1879, which occurs along European coasts; both species have small nuchal lappets, similar colour pattern, and body shape. The European species, however, has only 6 pentacuspid teeth on the trepan, and the segment that bears the proventricle is distinctly larger than other segments (San Martín, 2003). We are thus describing the Australian material as a new species. Haswell (1920) also reported some specimens 10 mm long, with 14–30 segments, these were not available for examination and because of their size we suggest that they probably represent another species.

Habitat. Occurring among bryozoans and others colonial animals, in shallow depths.

Distribution. Australia (New South Wales).

Etymology. The specific name refers to the highly denticulated trepan.

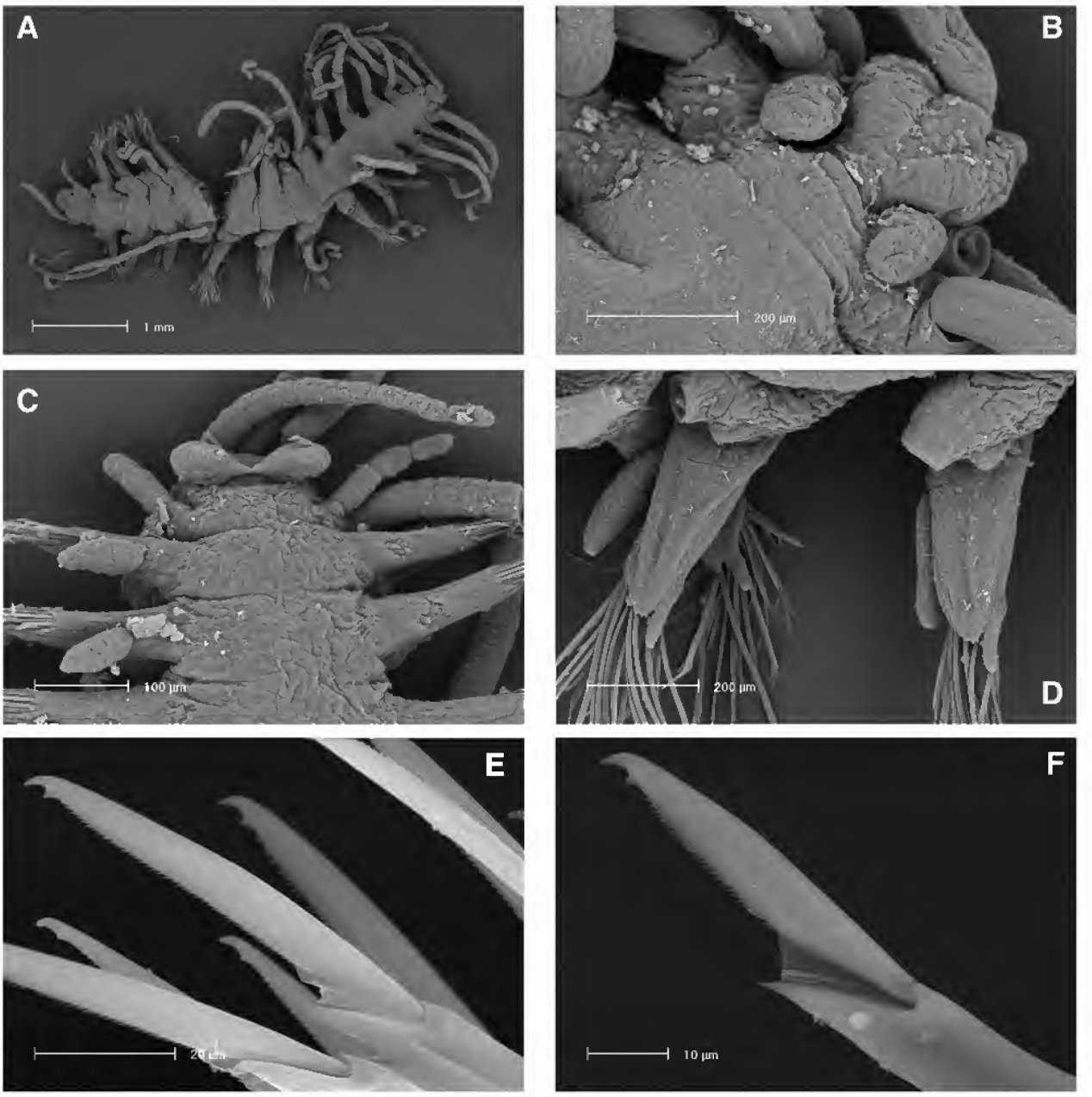


Fig. 4. SEM of *Amblyosyllis multidenticulata* n.sp. (*A*) complete specimen; (*B*) nuchal lappets; (*C*) anterior end, ventral view; (*D*) midbody parapodia, dorsal view; (*E*) superior compound chaeta; (*F*) inferior compound chaeta. AM W26323 (paratypes).

Amblyosyllis vesiculosa Hartmann-Schröder, 1989

Fig. 5A–C

Amblyosyllis vesiculosa Hartmann-Schröder, 1989: 25, figs 28–33.

Material examined. AUSTRALIA: NEW SOUTH WALES: Lake Macquarie, 33°03'S 151°38'E algae & epibionts, intertidal, coll. G. Hartmann-Schröder, holotype (HZM P-19661).

Description. Specimen complete, but broken in two pieces, in good condition. Body small, 2 mm long, 0.2 mm wide, with 13 chaetigers. Prostomium rounded; 4 eyes in trapezoidal arrangement. Antennae inserted on anterior margin of prostomium, median one with about 11 articles, lateral ones with about 7 articles (Fig. 5A). Palps ventrally folded, not visible dorsally. Nuchal lappets rounded, extending to anterior margin of chaetiger 1 (Fig. 5A). Peristomium visible dorsally; tentacular cirri similar to antennae; dorsal tentacular cirri with about 12 articles, ventral ones with 2–3 articles. Dorsal cirri about twice width of body, distinctly articulated, with about 12–14 articles; large, hyaline inclusions common throughout cirri and antennae (Fig. 5A). Ventral cirri, rounded, similar length to parapodial lobes, sometimes with large inclusions. Parapodial lobes length similar to body width, blunt, distally bilobed (Fig. 5B). Parapodia with compound chaetae, about 13–15 anteriorly, 9 posteriorly, heterogomph, with short, bidentate blades, with small dorsoventral gradation in length, with fine spines on margin (Fig. 5C). Pharynx, strongly coiled, extending to chaetiger 5 (Fig. 5A); trepan

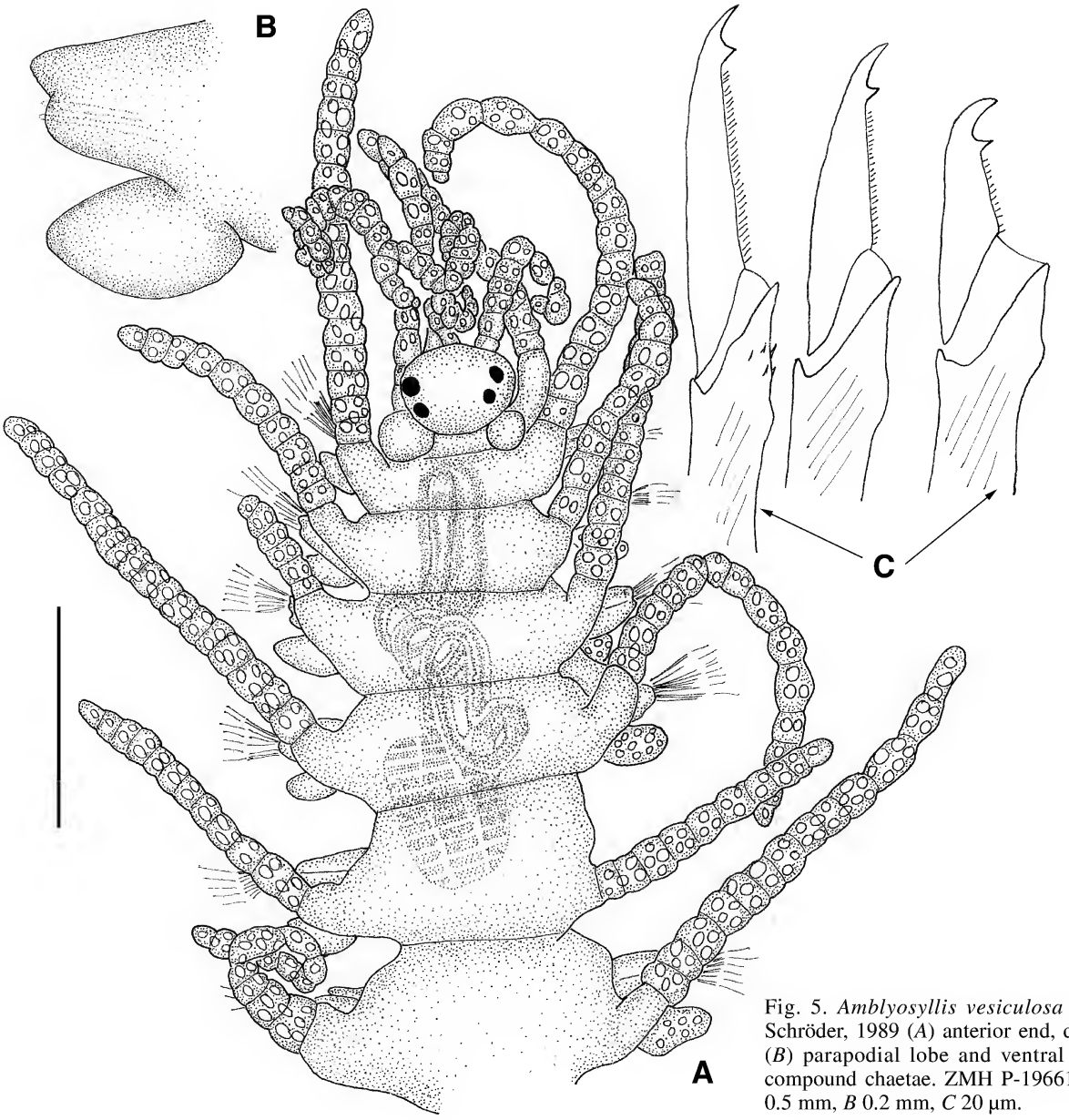


Fig. 5. *Amblyosyllis vesiculosa* Hartmann-Schröder, 1989 (*A*) anterior end, dorsal view; (*B*) parapodial lobe and ventral cirrus; (*C*) compound chaetae. ZMH P-19661. Scales: *A* 0.5 mm, *B* 0.2 mm, *C* 20 µm.

small, formed by 6 unidentate teeth (according to original description by Hartmann-Schröder, 1989), not verified. Proventricle on chaetiger 5, about length of segment, with about 14 muscle cell rows. Pygidium compact, with 2 coiled anal cirri.

Habitat. Occurring on algae, intertidally.

Distribution. Australia (New South Wales).

Genus *Anoplosyllis* Claparède, 1868

Anoplosyllis Claparède, 1868: 214.—San Martín, 2003: 134.

Type species. *Anoplosyllis edentula* Claparède, 1868, by monotypy.

Diagnosis. Body small, (<5 mm in length), with up to 30 chaetigers. Prostomium rectangular, similar width to anterior segments, with 2 pairs of eyes and 2 anterior eyespots. Three antennae. Palps small, fused basally, without median furrow. Nuchal organs as 2 ciliated grooves between prostomium and peristomium. Two pairs of tentacular cirri. Antennae, tentacular and dorsal cirri smooth, club-shaped, tapered basally, longer than parapodial lobes. Compound chaetae heterogomph, blades slender, elongate, unidentate or indistinctly bidentate. Dorsal and ventral simple chaetae present on some parapodia. Pharynx shorter than proventricle, unarmed. Proventricle large, almost as wide as body. Some species brood eggs in gelatinous masses.

Remarks. Fauvel (1923) synonymized *Anoplosyllis* with *Syllides*. Species of *Syllides*, however, have long, articulated cirri from chaetiger 3, and bidentate compound chaetae. Although these genera are closely related, San Martín (2003) proposed the resurrection of *Anoplosyllis*, and transferred species of *Syllides* with smooth dorsal cirri into the genus.

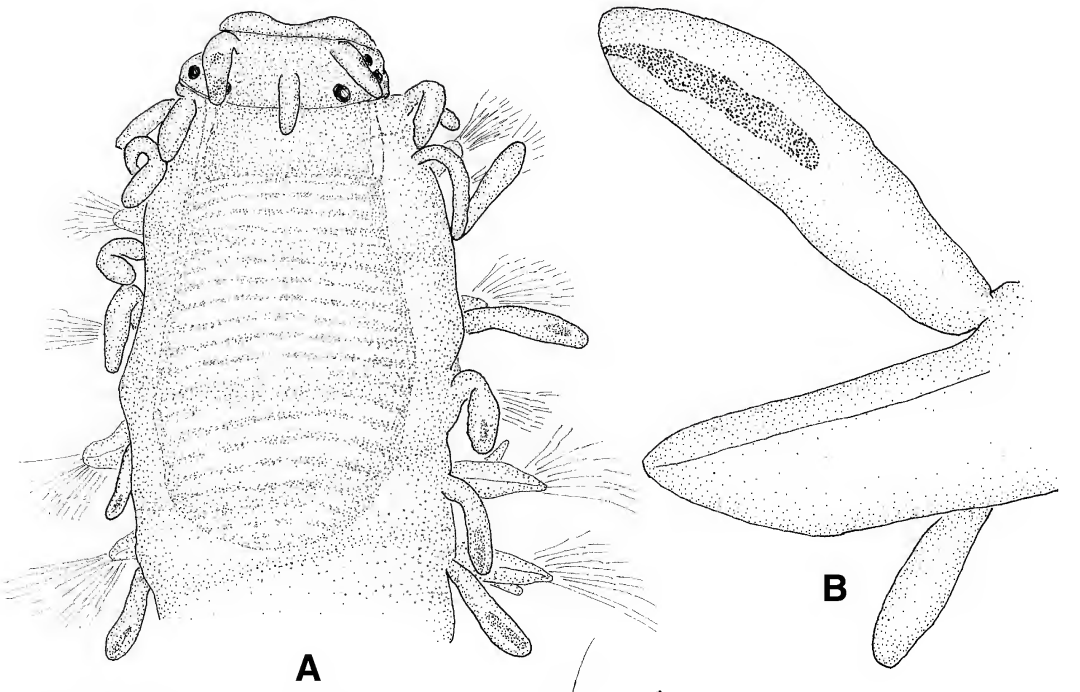


Fig. 6. *Anoplosyllis sexoculata* (Hartmann-Schröder, 1962) (*A*) anterior end, dorsal view; (*B*) midbody parapodium; (*C*) compound chaetae, midbody; (*D*) dorsal simple chaeta; (*E*) acicula; (*F*) ventral simple chaeta. *A,B*: AM W24700; *C–F*: AM W7465. Scale: *A* 0.18 mm, *B* 48 µm, *C–F* 20 µm.

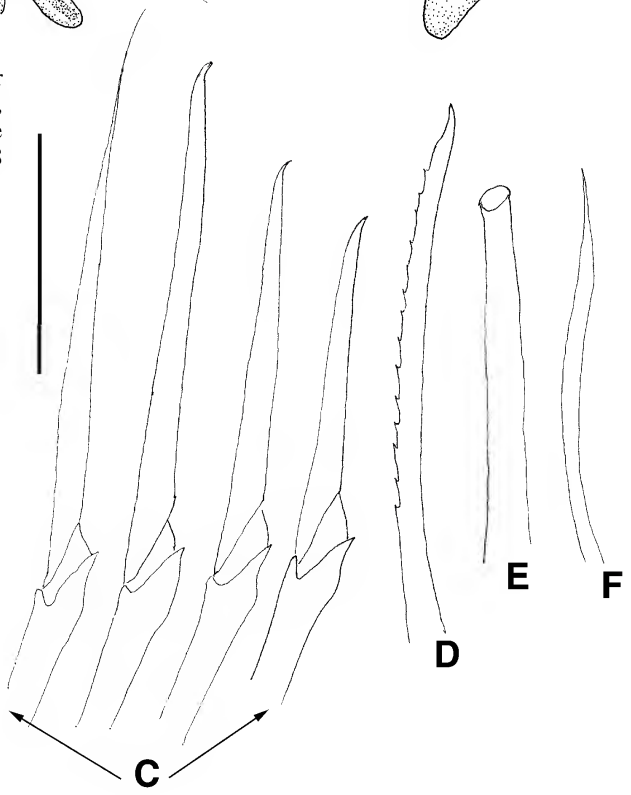
Anoplosyllis sexoculata (Hartmann-Schröder, 1962) n.comb.

Fig. 6A–F

Syllides sexoculata Hartmann-Schröder, 1962: 97, figs 78–80; 1974: 128; 1989: 27.

Material examined. AUSTRALIA: NEW SOUTH WALES: Between Liverpool Reach and Upper Half Moon Reach, Hawkesbury R., 33°25'S 150°55'E, coarse sand, 20 m, coll. A. Jones & party, 26 Aug 1980, 2 (AM W24699); Lower Half Moon Reach, Hawkesbury R., 33°25'S 150°57'E, coll. A. Jones & party, 26 Aug 1980, 1 (AM W24700); Tuross R., at Princes Hwy, Bodalla, 36°04'S 150°04'E, coll. D.F. Boesch, 23 May 1972, 1 (AM W7465). VICTORIA: Lakes Entrance, 33°05'S 151°40'E, 1 (HZM P-20037). CHILE: Niebla bei Valdivia, 39°46'S 73°150'W, holotype (HZM P-14673), 3 paratypes (HZM P-14674).

Description. Body up to 2 mm long with 20 chaetigers; complete specimen 1.4 mm long, 0.2 mm wide, 20 chaetigers. Prostomium oval, more than twice as wide as long; 4 eyes arranged in open trapezoidal pattern and 2 distinct anterior eyespots, similar in size to eyes (Fig. 6A). Antennae short, similar to width of prostomium, club-shaped; median antenna inserted between posterior eyes, lateral antennae near anterior margin of prostomium (Fig. 6A). Palps small, shorter than prostomium. Tentacular cirri similar to antennae, dorsal ones longer than ventral ones. Dorsal cirri similar to antennae and tentacular cirri (Fig. 6A), smooth, club-shaped, slightly longer than parapodial lobes, some with distinct dark inclusion (Fig. 6B), which opens via terminal pore. Parapodial lobes elongate; ventral cirri digitiform, shorter than parapodial lobes (Fig. 6B).



Compound chaetae heterogomph, smooth, slender, blades elongate, thin, unidentate, smooth (Fig. 6C), numbering 12–18 per parapodium, with dorsoventral gradation in length of blades, 48 µm in length dorsally, 29 µm in length ventrally. Dorsal simple chaetae from chaetiger 1, slender, unidentate, with minute spines on margin (Fig. 6D). Ventral simple chaetae on posterior chaetigers, similar to dorsal simple chaetae, but thinner and smooth (Fig. 6F). Aciculae solitary, slender, distally rounded (Fig. 6E). Pharynx partially everted, short, probably through 1–2 chaetigers. Proventricle, massive, through 4 segments (Fig. 6A); number of muscle cell rows not possible to assess. Pygidium small, triangular, with 2 filiform anal cirri and compact median papilla.

Remarks. The Australian material is represented by a few juvenile individuals and while they closely resembles the type material of *Anoplosyllis sexoculata* from southern Chile, they possess a shorter proventricle. At this stage we are referring them to this species, but mature individuals are really needed to confirm this.

Habitat. Occurring interstitially in fine to coarse sand, on algae, on colonies of sabellariids; intertidally to about 20 m.

Distribution. Southern Chile, Namibia, Australia (Victoria, New South Wales).

Genus *Astreptosyllis* Kudenov & Dorsey, 1982

Astreptosyllis Kudenov & Dorsey, 1982: 575.

Type species. *Astreptosyllis acrassiseta* Kudenov & Dorsey, 1982, by original designation.

Diagnosis. Body of meiofaunal size. Prostomium with 2 pairs of eyes and 3 antennae. Palps fused basally, small but visible dorsally without median furrow. Nuchal organs as 2 ciliated grooves between prostomium and peristomium. Two pairs of tentacular cirri. Antennae, tentacular cirri and dorsal cirri of 2 anterior chaetigers unarticulated, club-shaped, slender basally and distally slightly inflated, longer than body width; from chaetiger 3 onwards, dorsal cirri articulated, articles elongated to pyriform, with dark, glandular inclusions. Parapodial lobes subrectangular on anterior parapodia, conical and elongated from midbody; ventral cirri short and broad on anterior parapodia, posteriorly becoming more elongated, digitiform. Compound chaetae heterogomph or hemigomph falcigers. Dorsal simple chaetae thick, provided with distal, longitudinally striated hood. Ventral simple chaetae sometimes present on far posterior parapodia, but usually lacking. Pharynx unarmed, with distal crown of soft papillae. Pygidium with 2 anal cirri.

Remarks. The genus is only known from Australia. Details on reproduction unknown, probably it reproduces as other similar genera by epigamy.

Key to Australian species of *Astreptosyllis*

1 Compound chaetae similar throughout ..... *A. similiseta*

—— Compound chaetae of chaetigers 1–6 enlarged, hemigomph, with short, thick blades (Fig. 7E), different to compound chaetae of other parapodia (Fig. 7G) ..... *A. acrassiseta*

Astreptosyllis acrassiseta Kudenov & Dorsey, 1982

Figs 7A–I, 8A–F

Astreptosyllis acrassiseta Kudenov & Dorsey, 1982: 576, fig. 1.

Material examined. AUSTRALIA: NEW SOUTH WALES: Off Bass Point, 34°36'S 150°54'E, 50 m, 1 Feb 1990, 1 (AM W22995). VICTORIA: Port Phillip Bay, 38°16.3'S 144°41.5'E, medium sand, 13 m, Feb 1971, 1 paratype, (AM W18587). WESTERN AUSTRALIA: Ned's Camp, Cape Range National Park, 21°59'S 113°55'E, limestone reef near shore, fine sediment & sand from patches in reef, 1 m, coll. H.E. Stoddart, 2 Jan 1984, 1 (AM W26780).

Description. Body up to 3.1 mm long, 0.3 mm wide, with 42 chaetigers. Prostomium rectangular, 2 pairs of eyes in trapezoidal arrangement; antennae slightly club-shaped, unarticulated, usually missing; median antenna arising from posterior margin of prostomium, between posterior eyes, lateral antennae originating between anterior eyes. Palps large, similar in length to prostomium, basally totally fused (Figs 7A, 8A), directed anteriorly, provided with distal constriction. Tufts of cilia on lateral areas of prostomium and peristomium (Fig. 7A). Tentacular cirri and dorsal cirri of subsequent 2 segments similar to antennae; dorsal cirri from chaetiger 3 articulated (Figs 7A, 8A), slender, slightly longer than body width, with about 6–10 elongated articles, some with 1–2 granular, dark inclusions (Fig. 7A,C). Parapodia of anterior segments relatively broad in contrast, to posterior ones, distally truncated, with some distal incisions (Fig. 7B); becoming elongated and conical from proventricular segments onwards, with dorsal band of long cilia (Fig. 7C). Ventral cirri of anterior parapodia broad, shorter than parapodial length, becoming greatly elongated posteriorly, longer than parapodial length, arising from about middle of ventral side of parapodial lobes (Fig. 7C). Anterior 1–6 chaetigers each with 8–10, sometimes 12, compound chaetae with enlarged shafts, hemigomph articulation, with short, stout, broad blades, apparently unidentate or bifid, with distal incision (Figs 7E, 8B), about 8–15 µm long. From chaetiger 7 onwards, parapodia with 5–8 compound chaetae with shafts much slender than those of anterior chaetae, heterogomph, with fine spines on margin (Figs 7G, 8C,D), and blades slender, unidentate, some with distal hood, with minute spines on margin, and dorsoventral gradation in length of blades within fascicle (Fig. 8C), 27 µm in length dorsally and 15 µm in length ventrally; under SEM, margin with several rows of spines (Fig. 8E) and distal hood composed of minute spines (Fig. 8E). Acicula solitary, distally knobbed (Fig. 7B,H). Dorsal simple chaetae from chaetiger 1, thick, tip tapered, blunt, covered with longitudinally striated, rounded hood (Fig. 7D,F); under SEM, dorsal simple chaetae with "*Banksia*-like" or "artichoke-like" appearance. Ventral simple chaetae usually absent, but one specimen with single thin, smooth, filiform, ventral simple chaeta (Fig. 7I) on each fascicle of last parapodium. Pharynx through about 7–8 segments, with crown of 10 soft papillae (Fig. 7A). Proventricle through about 7–8 segments, with 30–32 muscle cell rows. No specimens with anal cirri present, probably present on undamaged specimens.

Habitat. Occurring in median to coarse sand; from intertidal to 50 m.

Distribution. Australia (Victoria, New South Wales, Western Australia).

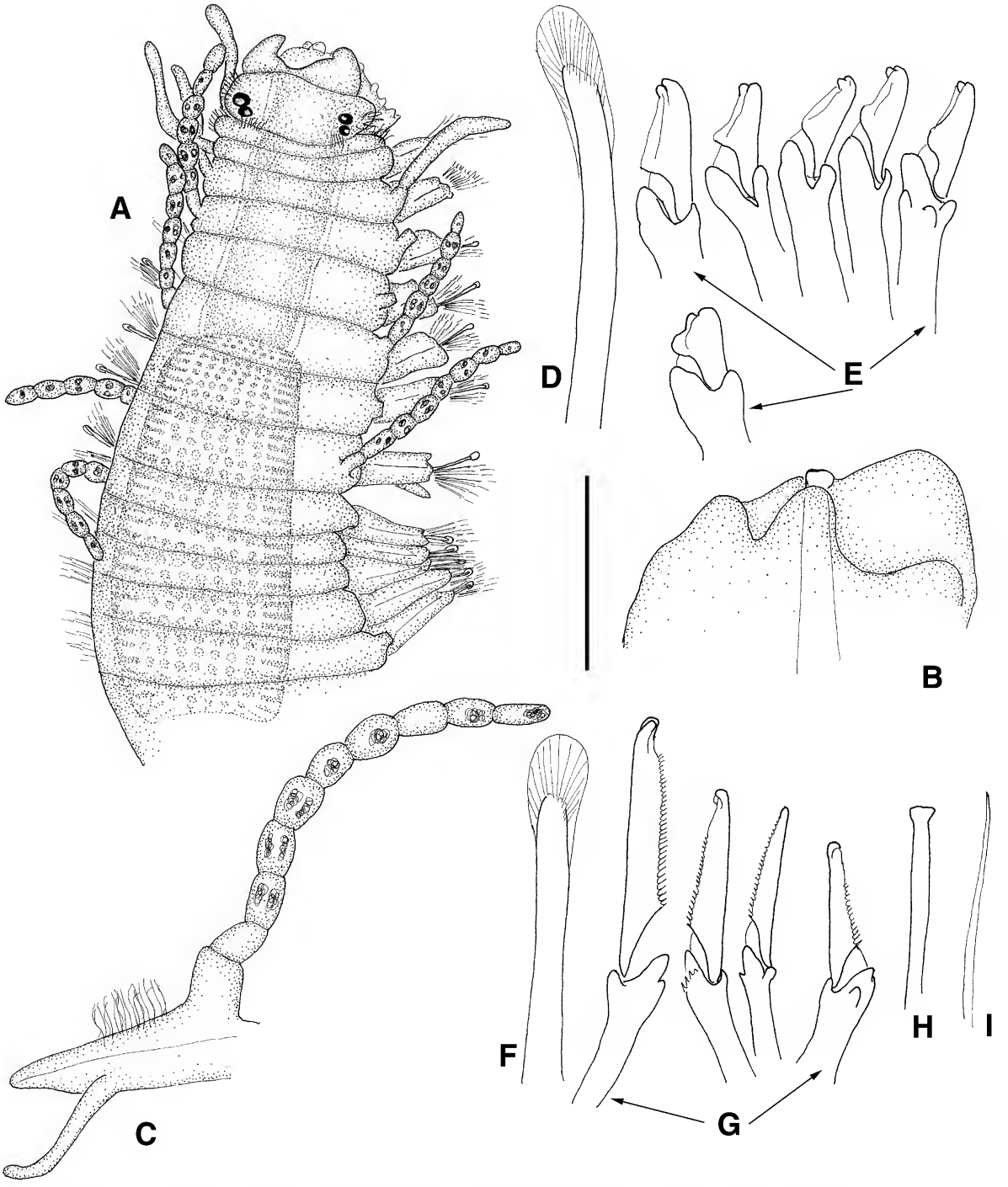


Fig. 7. *Astreptosyllis acrassiseta* Kudenov & Dorsey, 1982 (*A*) anterior end, dorsal view (antennae and some tentacular and dorsal cirri missing); (*B*) anterior parapodial lobe and acicula, dorsal view; (*C*) posterior parapodium; (*D*) dorsal simple chaeta, anterior parapodium; (*E*) compound chaetae, anterior parapodium; (*F*) dorsal simple chaeta, midbody; (*G*) compound chaetae, midbody; (*H*) acicula, midbody; (*I*) ventral simple chaeta. AM W26780. Scales: *A* 0.18 mm; *C* 92 µm; *B, D–I* 20 µm.

Astreptosyllis similiseta Hartmann-Schröder, 1986

Fig. 9A–H

Astreptosyllis similiseta Hartmann-Schröder, 1986: 40, figs 16–21.

Material examined. AUSTRALIA: SOUTH AUSTRALIA: Port Augusta, 32°30'S 137°13'E, intertidal sediments, 6 Dec 1975, holotype (HZM P-18624) and 3 paratypes (HZM P-18625), coll. G. Hartmann-Schröder.

Description. Body, delicate, fragile, entire, without colour markings, 1.8–2.0 mm long, 0.1 mm wide, with 23–28 chaetigers. Prostomium semi-circular, with 4 eyes in open trapezoidal arrangement; antennae fusiform to club-shaped, smooth; median antenna longer than combined length of prostomium and palps, inserted on middle of pharynx, between anterior eyes; lateral antennae similar in shape to median antenna, but shorter, inserted near anterior margin of prostomium (Fig. 9A). Palps small, shorter than

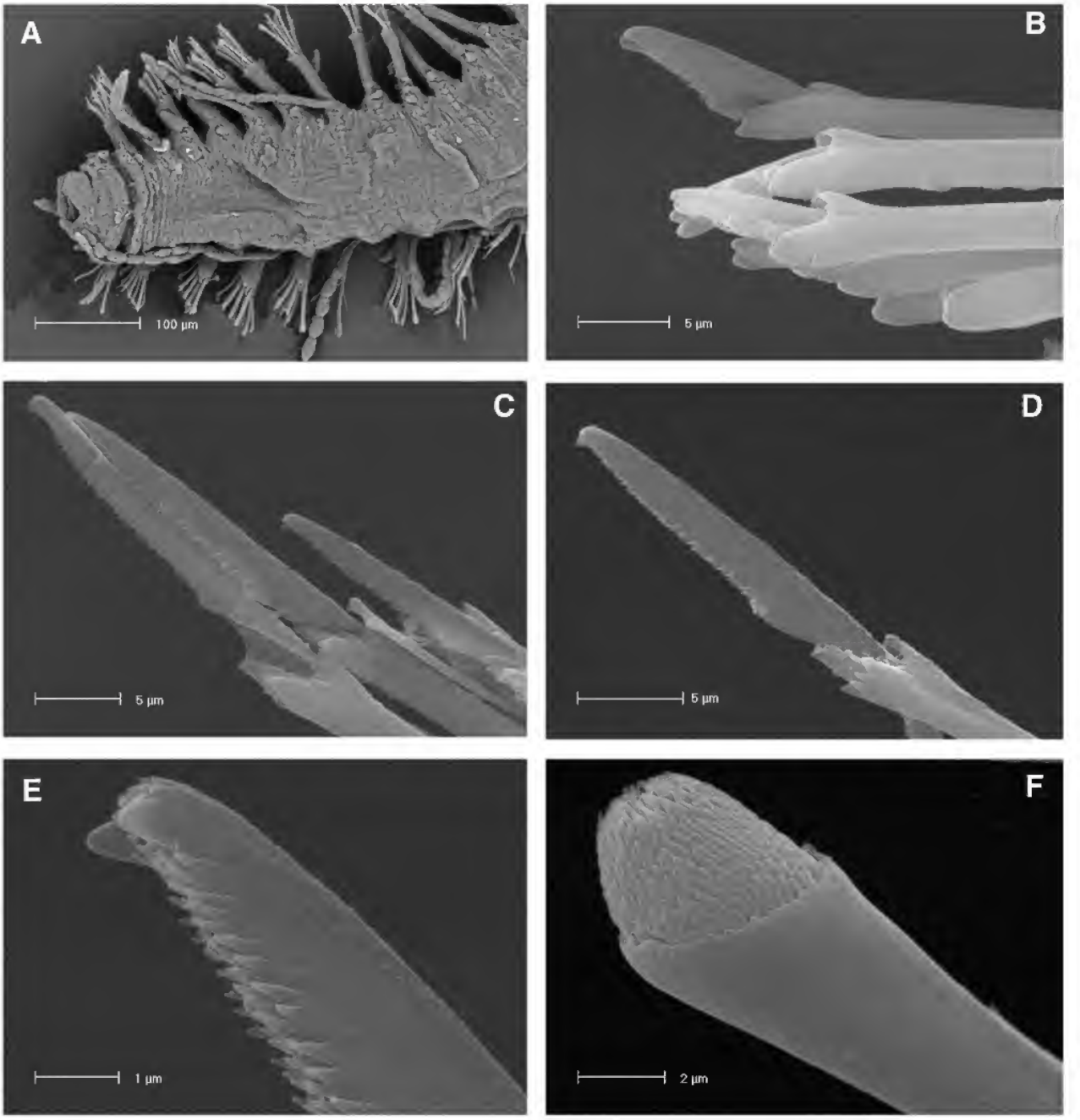


Fig. 8. SEM of *Astreptosyllis acrassiseta* Kudenov & Dorsey, 1982 (*A*) anterior end, dorsal view (antennae and some tentacular and dorsal cirri missing); (*B*) compound chaetae, anterior parapodium; (*C*) compound chaetae, midbody; (*D*) dorsalmost compound chaeta, posterior parapodium; (*E*) detail of tip of the same; (*F*) detail of distal end of dorsal simple chaeta, midbody. AM W26780.

prostomium, fused basally (Fig. 9A). Peristomium similar in size to subsequent segments; tentacular cirri smooth, slightly club-shaped (Fig. 9A); dorsal tentacular cirri similar in length to lateral antenna, ventral ones shorter than dorsal ones. Dorsal cirri of anterior 2 chaetigers similar in shape to antennae and tentacular cirri, and slightly longer; dorsal cirri from chaetiger 3 onwards articulated, with some dark granular inclusions on some articles (Fig. 9A,B), 5–7 articles on midbody chaetigers. Parapodia slender, elongated; ventral cirri digitiform, longer on posterior parapodia (Fig. 9B) becoming of similar length to parapodial lobes. Compound chaetae heterogomph falcigers, with conspicuous spines subdistally on shafts, and unidentate blades with short, apparently smooth spines on margin. Anterior parapodia (1–5 chaetigers) each with several compound chaetae, with slight dorsoventral gradation in length of blades within fascicle, 40 µm in length dorsally, 20 µm in length ventrally (Fig. 9D); on midbody blades of compound chaetae longer, more marked gradation (65 µm dorsally and 23 µm ventrally) (Fig. 9F); posterior parapodia with less marked dorsoventral gradation in length of blades within fascicle (40 µm dorsally and 23 µm ventrally) (Fig. 9G). Dorsal simple chaetae thick, distally unidentate, with distinct distal hood longitudinally striated, similar throughout (Fig. 9C,E,H), present from anterior parapodia. Ventral simple chaetae absent. Pharynx through about 5 segments; proventricle through 4.5 segments (Fig. 9A), with 38–40 muscle cell rows. Pygidium rounded, with single digitiform

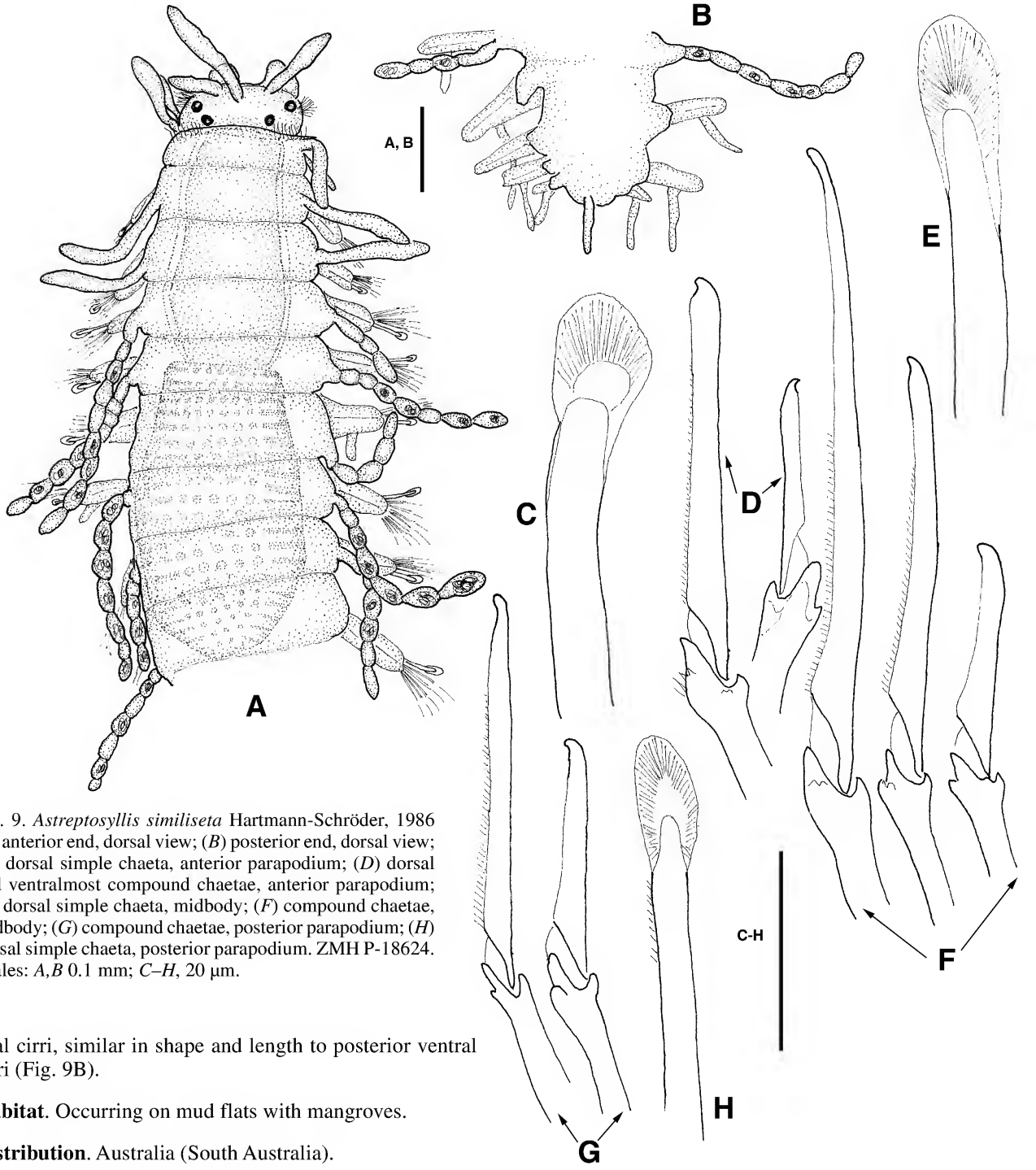


Fig. 9. *Astreptosyllis similiseta* Hartmann-Schröder, 1986 (*A*) anterior end, dorsal view; (*B*) posterior end, dorsal view; (*C*) dorsal simple chaeta, anterior parapodium; (*D*) dorsal and ventralmost compound chaetae, anterior parapodium; (*E*) dorsal simple chaeta, midbody; (*F*) compound chaetae, midbody; (*G*) compound chaetae, posterior parapodium; (*H*) dorsal simple chaeta, posterior parapodium. ZMH P-18624. Scales: *A,B* 0.1 mm; *C–H*, 20 μm.

anal cirri, similar in shape and length to posterior ventral cirri (Fig. 9B).

Habitat. Occurring on mud flats with mangroves.

Distribution. Australia (South Australia).

Genus *Eusyllis* Malmgren, 1867

Eusyllis Malmgren, 1867: 40.
Eudontosyllis Knox, 1960: 105.

Type species. *Eusyllis blomstrandi* Malmgren, 1867

Diagnosis. Body of medium to small size (10 to <5 mm in length), cylindrical. Prostomium with 4 eyes and sometimes 2 anterior eyespots. Three antennae. Palps either entirely free or fused just basally. Nuchal organs as 2 ciliated grooves, ciliation extending sometimes to prostomium and peristomium, as well as other segments. Two pairs of tentacular cirri. Antennae, tentacular and dorsal cirri non-articulated, sometimes rugose, with pseudoarticulate appearance. Compound chaetae; dorsal and ventral simple chaetae on some parapodia. Pharynx with mid-dorsal tooth, usually large and conspicuous, and incomplete crown of small denticles, anteriorly pointing. Pygidium with 2 anal cirri. Reproduction by epigamy (Garwood, 1991).

Remarks. *Eusyllis* is characterized by having an incomplete trepan on the pharynx, with all teeth anteriorly directed, and a mid-dorsal, usually large, tooth. Species of this genus are typically large, even so the denticles of the trepan are small and sometimes difficult to observe, which can lead to misidentifications. *Eusyllis brevicirrata* Knox & Cameron,

1971 from New Zealand, reported in Australia by Hartmann-Schröder (1985), reproduces by schizogamy (San Martín, pers. observ., on Australian material) so we suggest that this species represents a member of the subfamily Syllinae probably an undescribed genus (San Martín *et al.*, in prep.). Australian material agrees with the original description based on New Zealand material. *Eudontosyllis* has been recently proposed as a synonymy of *Eusyllis* by Glasby *et al.*, (in press).

Key to Australian species of *Eusyllis*

1 Ventral cirri of chaetiger 1 enlarged, flattened leaf-like (Fig. 15B) ..... *E. lamelligera*

—— Ventral cirri of chaetiger 1 not enlarged, flattened leaf-like 2

2 Aciculae from midbody greatly enlarged, distally curved, extending beyond parapodial lobes (Fig. 10G). Compound chaetae distinctly bidentate (Fig. 10F) ..... *E. assimilis*

—— Aciculae not modified (Fig. 13E). Compound chaetae unidentate (Fig. 13C) ..... *E. kupffferi*

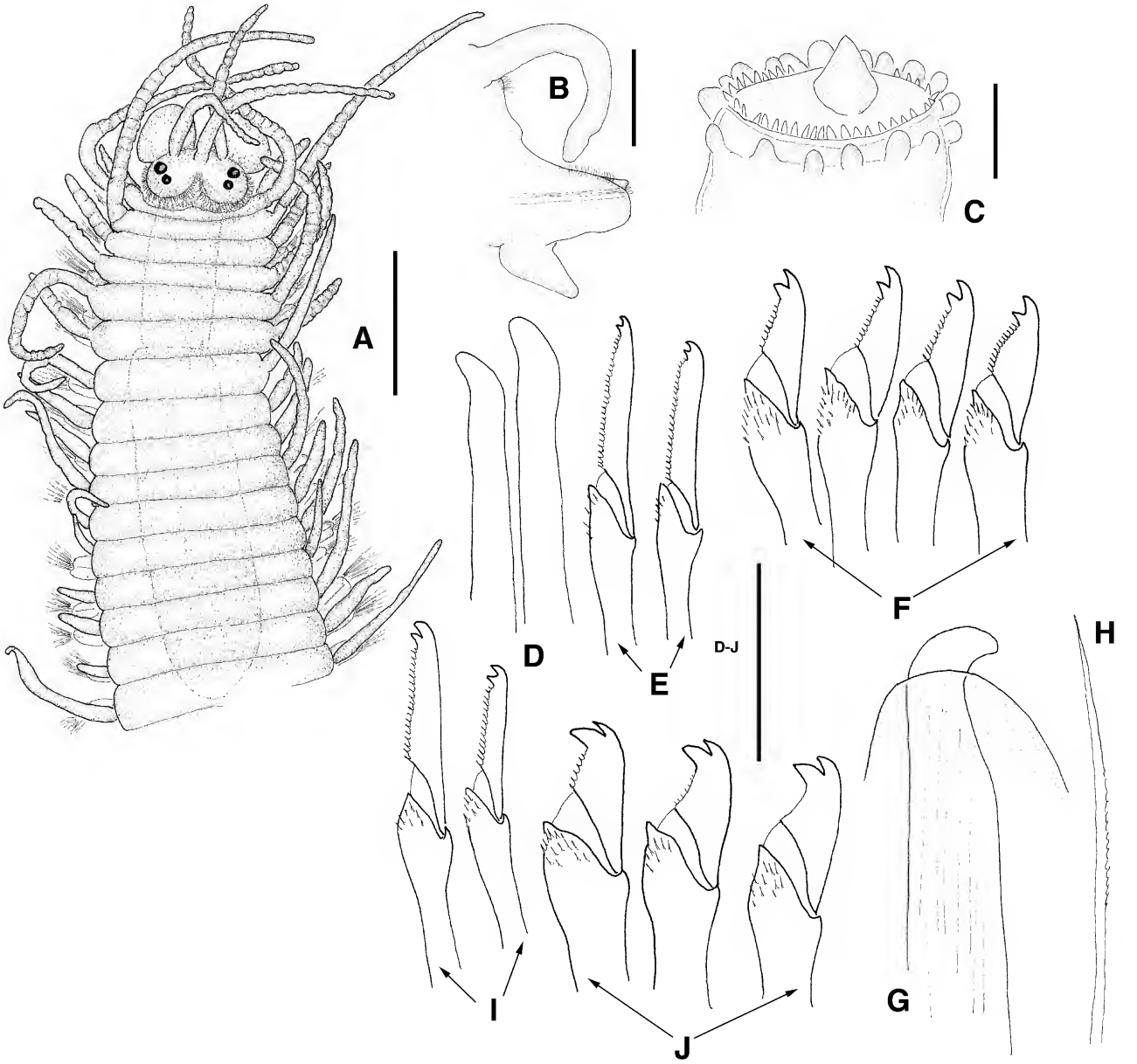


Fig. 10. *Eusyllis assimilis* Marenzeller, 1875 (*A*) anterior end, dorsal view; (*B*) midbody parapodium; (*C*) pharyngeal opening; (*D*) aciculae, anterior parapodium; (*E*) dorsalmost compound chaetae, anterior parapodium; (*F*) remaining compound chaetae, anterior parapodium; (*G*) acicula, posterior parapodium; (*H*) dorsal simple chaeta; (*I*) dorsalmost compound chaetae, posterior parapodium; (*J*) remaining compound chaetae, posterior parapodium. AM W28878. Scales: *A* 0.4 mm, *B* 0.1 mm, *C* 0.1 mm, *D–J* 20 μm.

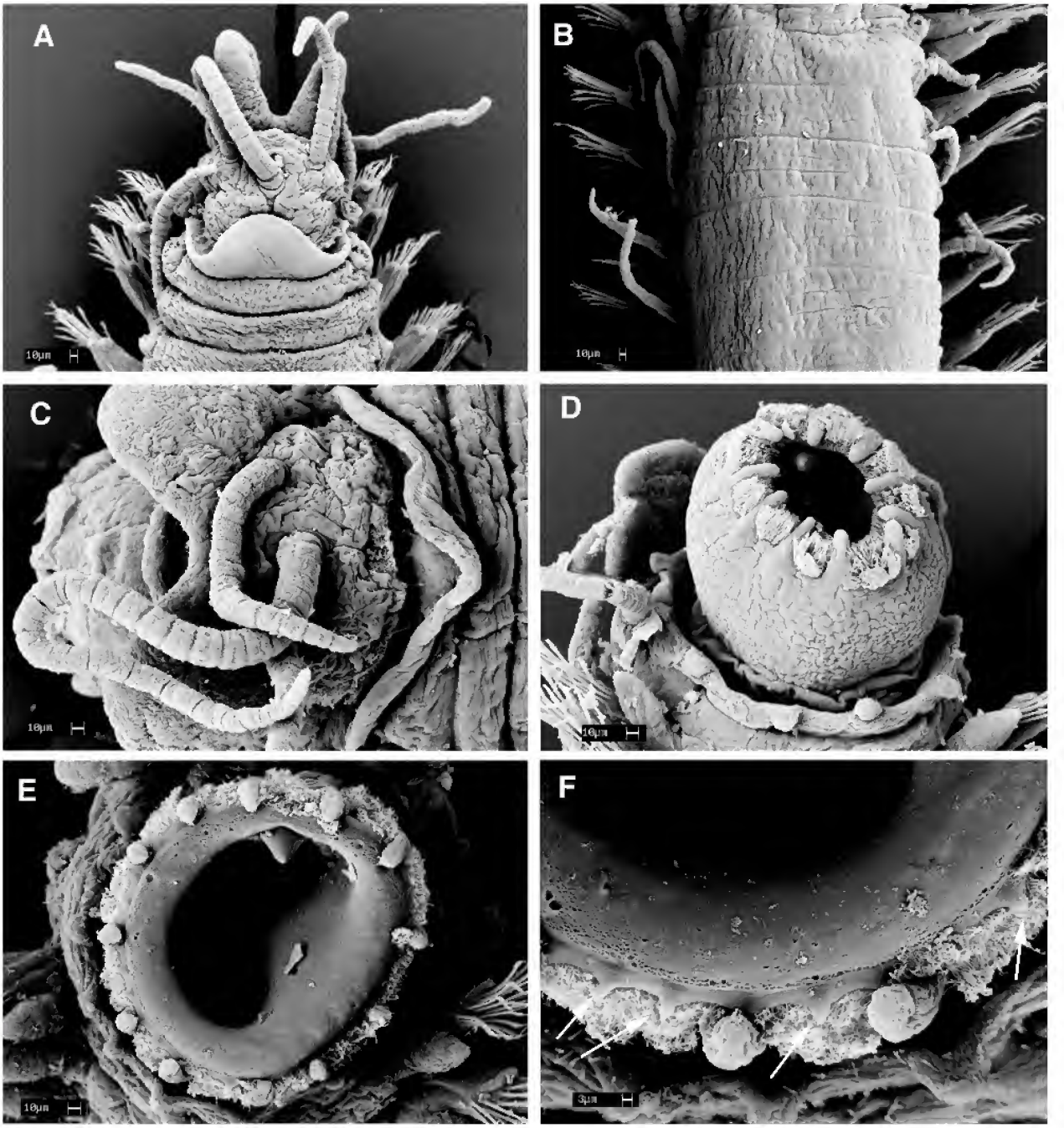


Fig. 11. SEM of *Eusyllis assimilis* Marenzeller, 1878 (*A*) anterior end, dorsal view; (*B*) midbody, dorsal view; (*C*) detail of prostomium, dorsal view; (*D*) everted pharynx; (*E*) pharyngeal opening; (*F*) detail of the same (arrows show denticles). AM W28878, W28879.

Eusyllis assimilis Marenzeller, 1875

Figs 10A–J, 11A–F, 12A–C

Eusyllis assimilis Marenzeller, 1875: 158, pl. 3, Fig. 2.—Fauvel, 1923: 294, fig. 112a–g.—San Martín, 2003: 114, figs 52, 53.
?*Eudontosyllis aciculata* Knox, 1960: 105, figs 113–117.

Material examined. AUSTRALIA: NEW SOUTH WALES: SW side of South Solitary Is. 30°12'S 153°16'E, coral rubble, 18 m, coll. R.T. Springthorpe, 24 Jun 1992, 1 (AM W28942); Taupo Seamount, Tasman Sea, 33°14.21'S 156°10.68'E, rough marl bottom, 133 m, coll. J.K. Lowry & party on RV "Franklin", 2 May 1989, 2 on SEM stub (AM W28878); Taupo Seamount, Tasman Sea, 33°16.85'S 156°09.15'E, limestone & sand, 244 m, coll. J.K. Lowry & party on RV "Franklin", 2 May 1989, 4 on SEM stub (AM W28879); Taupo Seamount, Tasman Sea, 33°16.85'S 156°09.15'E, limestone & sand bottom, 244 m, coll. J.K. Lowry & party on RV Franklin, 2 May 1989, 17 (AM W28925). SOUTH AUSTRALIA: Lowly Point, 33°00'S 137°47'E, subtidal, 1 (AM W26357); 4 km NW of 5th Creek, Port Pirie, Spencer Gulf, 33°12'S 137°55'E, subtidal, *Posidonia* sp. and *Amphibolus* spp, 4.6 m, T.J. Ward & party, Mar 1980, 1 (AM W28234). WESTERN AUSTRALIA: Red Bluff, Kalbarri, 27°42'S 114°09'E, mixed coralline algae on rocky shore, 3.5 m, coll. J.K. Lowry, 10 Jan 1984, several

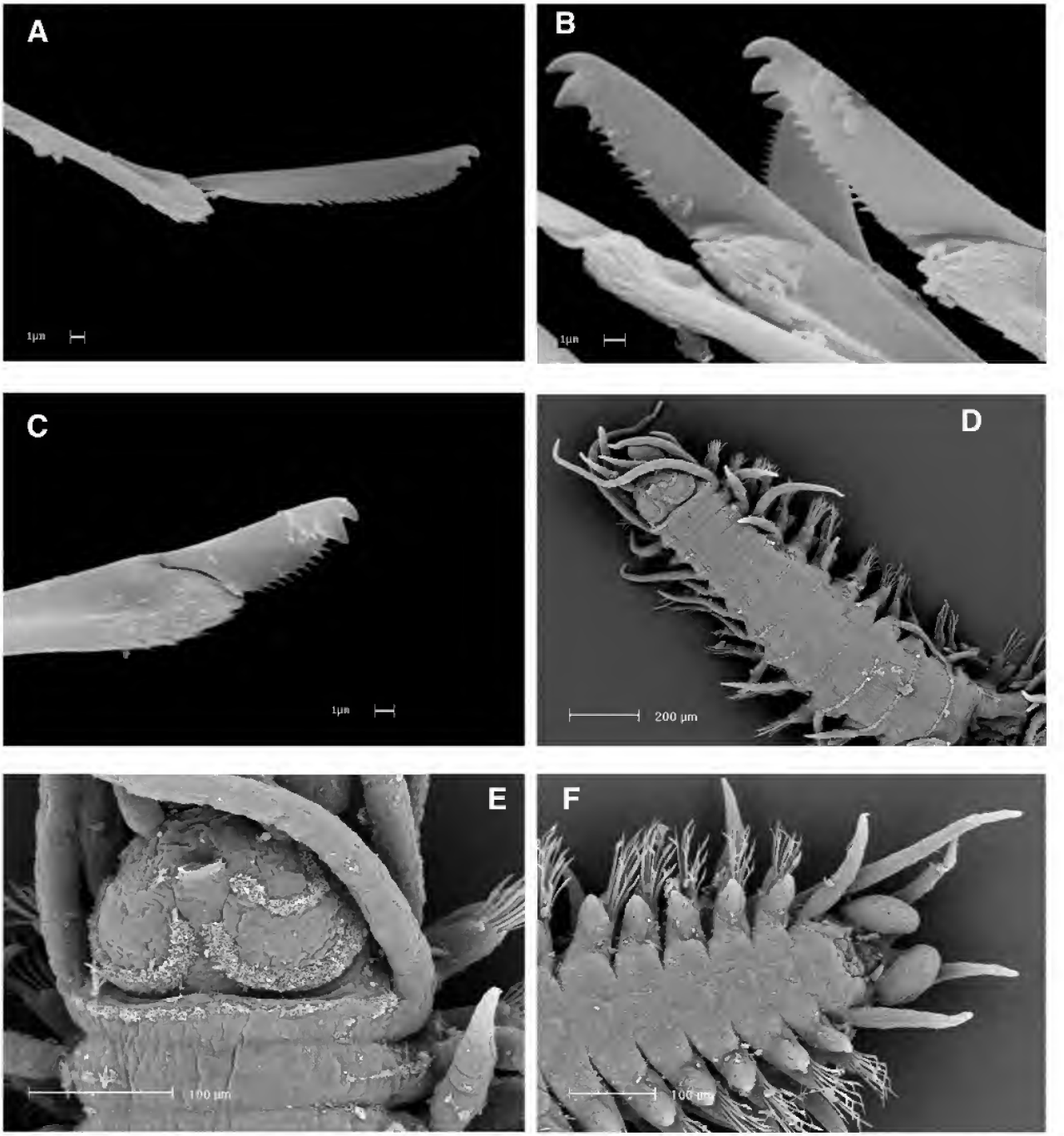


Fig. 12. SEM of *Eusyllis assimilis* Marenzeller, 1878 (*A*) dorsal compound chaeta, midbody; (*B*) compound chaetae, midbody; (*C*) compound chaeta, posterior parapodium. SEM of *Eusyllis kupfferi* Langerhans, 1879 (*D*) anterior end, dorsal view; (*E*) detail of prostomium and anteriormost segments, dorsal view; (*F*) anterior end, ventral view. *A–C*: AM W28878, W28879, *D–F*: AM W28952.

(AM W28941); Bundegi Reef near Point Murat, Exmouth Gulf, 21°49'S 113°11'E, orange finger sponge, 9 m, coll. J.K. Lowry, 4 Jan 1984, WA-398, 1 (AM W26738).

Additional material examined. Spain: Off Cabo Cros, Soller, Mallorca, Balearic Is., 39°38.50'N 02°25.13'E, dredged 59–61 m, 6 (MNCNM 8637); Off Ribadeo, Lugo, Galicia, 43°40.59'–43°40.25'N 7°02.77'–7°04.35'E, dredged 114–116 m, 8 (MNCNM 8643).

Description. Material examined small to medium size (10 to <5 mm length), described specimen 5 mm long, 0.54 mm wide, with 41 chaetigers (all incomplete specimens), fragile. Elsewhere; specimens exceeding 40 mm in length reported. Prostomium oval, deeply incised posteriorly, forming 2 distinct lobes, densely ciliated on margin (Figs 10A, 11A,C); 4 eyes in open trapezoidal arrangement; antennae long, slender, much longer than combined length of prostomium and palps, irregularly pseudoarticulated; lateral antennae inserted near anterior margin of prostomium, median antenna arising slightly posteriorly to lateral ones (Figs 10A, 11A,C). Palps broad, similar in length to prostomium or slightly longer. Peristomium shorter than subsequent segments; dorsal tentacular cirri long, similar in shape but longer than median antenna, ventral tentacular cirri about quarter length of dorsal ones. Occipital flap

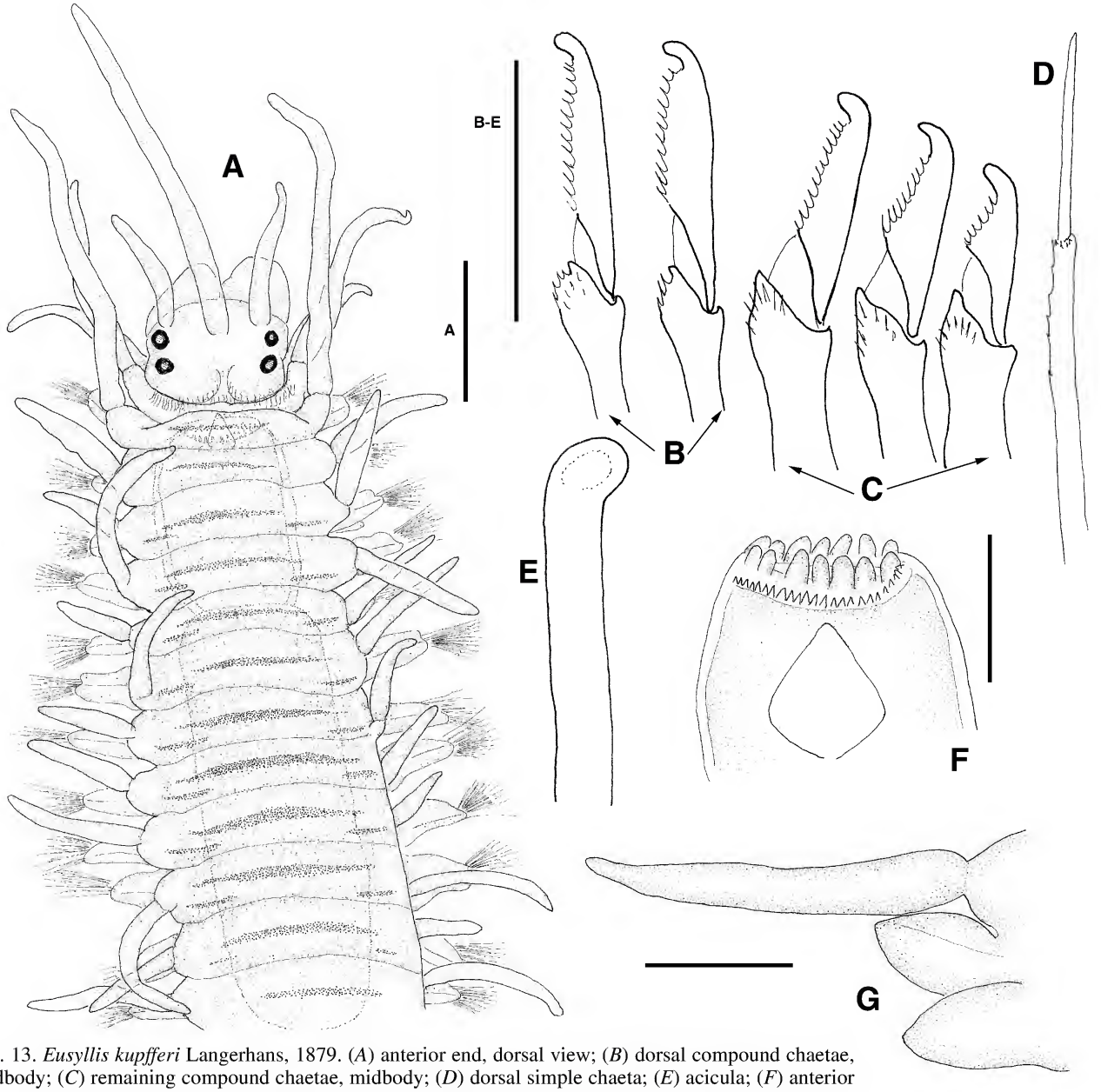


Fig. 13. *Eusyllis kupfferi* Langerhans, 1879. (*A*) anterior end, dorsal view; (*B*) dorsal compound chaetae, midbody; (*C*) remaining compound chaetae, midbody; (*D*) dorsal simple chaeta; (*E*) acicula; (*F*) anterior end of pharynx; (*G*) parapodium, midbody. *A,F*: AM W28404; *B–G*: AM W28408. Scales: *A* 0.2 mm, *B–E* 20 µm, *F* 0.1 mm, *G* 0.18 mm.

present (Fig. 11A,C). Dorsal cirri of chaetiger 1 elongated, longer than dorsal tentacular cirri, also indistinctly articulated; following dorsal cirri irregularly alternating long cirri, slightly longer than half of body width, and others distinctly shorter, all smooth, elongated, tapered (Figs 10A, 11B). Parapodia with prechaetal lobes. Parapodia dorsally with cilia; other groups of cilia dorsally along body close to dorsal cirri (Figs 10B, 11B). Ventral cirri triangular, shorter than parapodial lobes (Fig. 11B). Compound chaetae heterogomph falcigers, with shafts distally covered in numerous, thin spines. Two different types of compound chaetae present, one with slender, bidentate blades, both teeth similar, and short spines on margin (Figs 10E,I, 12A), located dorsally, others with shorter and larger blades, strongly bidentate, both teeth similar on anterior parapodia (Figs 10F, 12B), on posterior parapodia proximal tooth becoming longer and stouter, located more ventrally within bundles (Figs 10J, 12C). Anterior parapodia with 3 compound chaetae of slender type, blades about 20–22 µm in length, and 19–20 compound chaetae of broad type, blades about 15 µm in length. Posteriorly along body, number of compound chaetae decreases, posterior parapodia with 1–2 compound chaetae of slender type, blades 15–22 µm in length, and 6 of broad type, with prominent proximal tooth, and minute spines or smooth on margin, about 16 µm in length. Dorsal simple chaetae slender, capillaries, unidentate, with minute subdistal spines on margin (Fig. 10H), present only on posterior parapodia. Ventral simple chaetae not seen. Anterior parapodia with 2 slender aciculae, with slightly bent tip (Fig. 10D); posteriorly single aciculum present, thicker than anterior ones, distally bent and extending beyond parapodial lobes (Fig. 10G). Pharynx through about 7–8 segments; opening surrounded by a crown of 17–20 soft papillae and dense layer of cilia (Fig. 11D–F); plus crown of 10 smaller papillae basally (Fig. 11D); pharyngeal tooth large, located on anterior margin

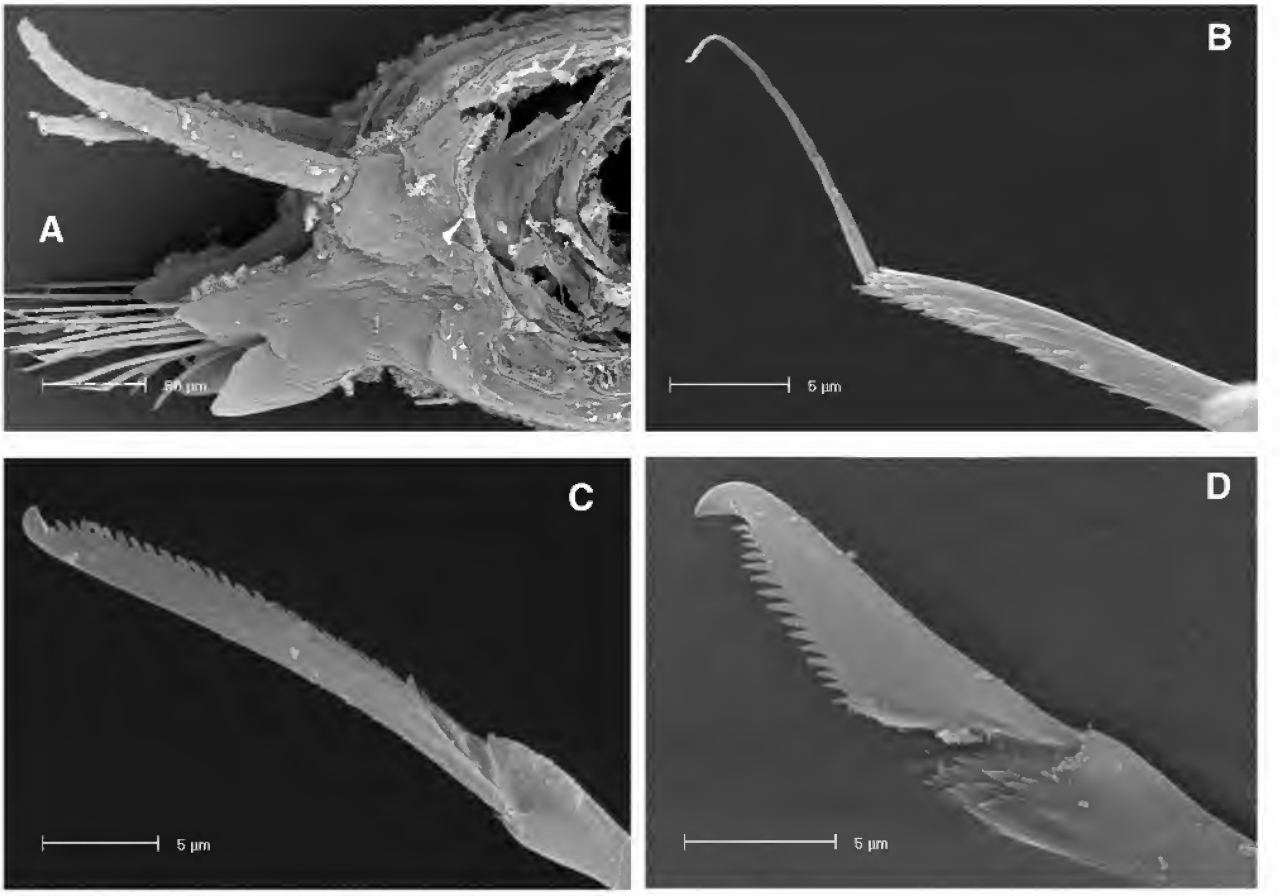


Fig. 14. SEM of *Eusyllis kupfferi* Langerhans, 1879 (*A*) right section of a midbody segment; (*B*) dorsal simple chaeta; (*C*) dorsalmost compound chaeta, anterior parapodium; (*D,E*) short compound chaetae, anterior parapodium. AM W28952.

(Fig. 10C); trepan incomplete, with variable number of teeth, ranging from few to up to 35 separate teeth present (Fig. 11F, arrows). Proventricle elongate, through about 10 segments, tapering posteriorly, with about 50 muscle cell rows.

Remarks. This species has been reported from a wide range of habitats and depths and material should be re-examined and a molecular study would be useful to confirm if this is a widely distributed species or a suite of sibling species. We believe that *Eudontosyllis aciculata* Knox, 1960, is identical with *E. assimilis* based on the description. We were unable, however, to borrow this material.

Habitat. Occurring in all kind of substrates, from intertidal to more than 500 m depth.

Distribution. North Atlantic, Mediterranean Sea, North Pacific, New Zealand, Australia (Western Australia, South Australia, New South Wales).

Eusyllis kupfferi Langerhans, 1879

Figs 12D–F, 13A–G, 14A–E

Eusyllis kupfferi Langerhans, 1879: 552, Fig. 14.—San Martín, 1990: 607, figs 12, 13.
Eusyllis autolytoides Hartmann-Schröder, 1991: 33, figs 47–53.
Odontosyllis multidentata Hartmann-Schröder, 1982: 64, figs 41–46; 1990: 51, fig. 17.

Material examined. AUSTRALIA: QUEENSLAND: SW Reef, Heron Is. 23°27'S 151°55'E, reef margin, algae, coral sand & coral debris, 3 Feb 1976, 2 paratypes of *Eusyllis autolytoides* Hartmann-Schröder, 1991, (AM W20387). NEW SOUTH WALES: Off old wharf, Richmond R., near Ballina, 28°52.5'S 153°33.6'E, drift algae, 6 m, coll. S.J. Keable, 5 Mar 1992, 4 (AM W28218); S ledge, Cook Is. 28°11.65'S 153°34.63'E, surface of massive sponges, 14 m, coll. R.T. Springthorpe, 9 Jun 1993, 1 (AM W28402); S ledge, Cook Is. 28°11.65'S 153°34.63'E, *Halimeda* sp., 13 m, coll. E.L.A. Ho, 9 Jun 1993, 1 (AM W28404); SW side of South Solitary Is. 30°12'S 153°16'E, coral rubble, 18 m, coll. R.T. Springthorpe, 24 Jun 1992, few (AM W28215); 1 km S of E end of Spectacle Is. Hawkesbury R., 33°32'S 151°07.5'E, muddy sand, 12 m, coll. A.R. Jones & A. Murray, 8 May 1984, 1 (AM W22149); Green Pt. Croppy Pt. Hawkesbury R., 33°33.5'S 151°14.5'E, mud, 6 m, coll. A. Jones & party, 22 Feb 1980, 1 (AM W196604); E end of Brooklyn Boat Channel, Hawkesbury R., 33°33'S 151°14'E, coll. A. Jones & party, 18 Dec 1979, 1 (AM W196606); E end of Brooklyn Boat Channel, Hawkesbury R., 33°33'S 151°14'E, coll. A. Jones & party, 16 May 1980, 1 (AM W196607); E end of Brooklyn Boat Channel, Hawkesbury R.,

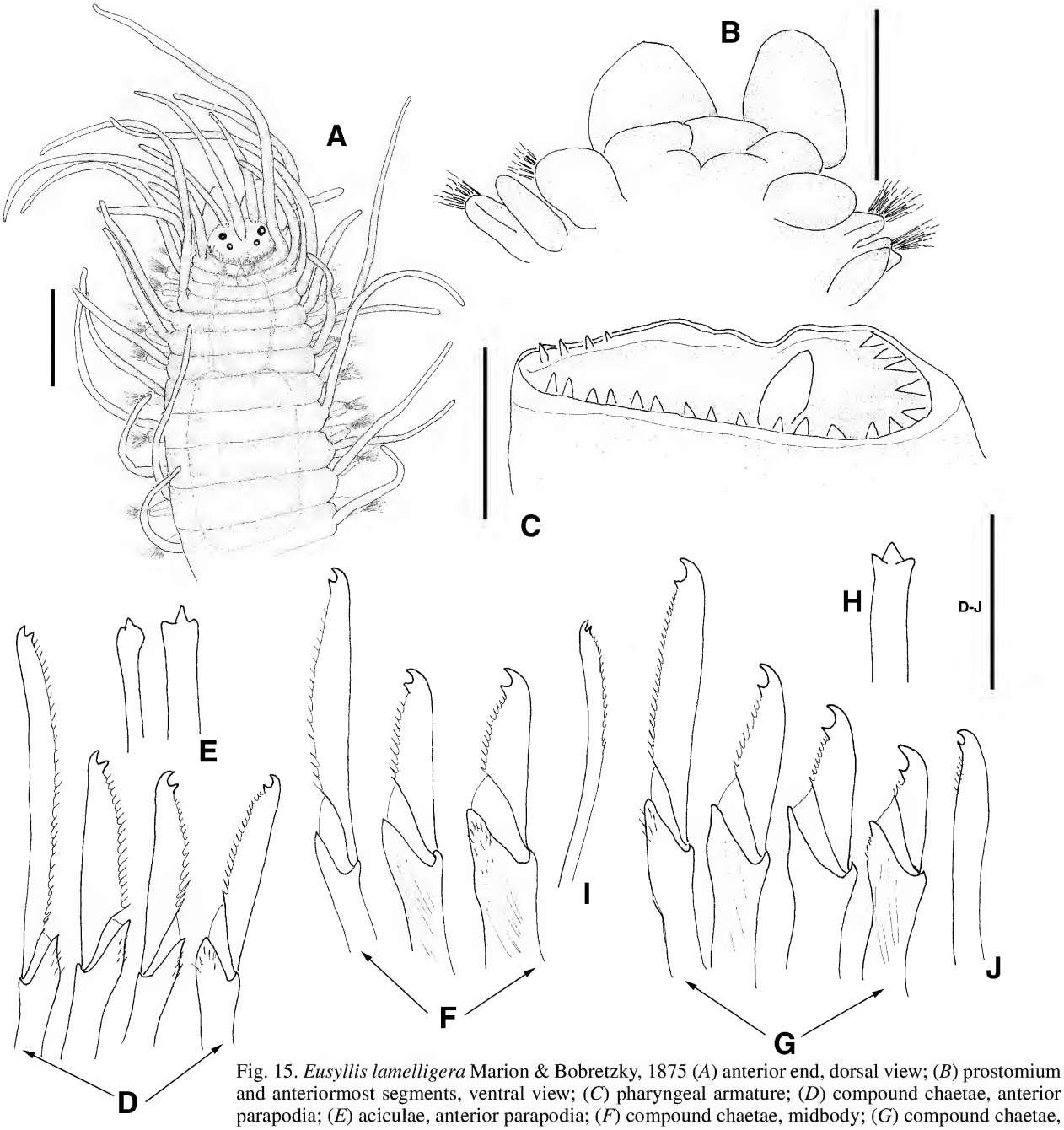


Fig. 15. *Eusyllis lamelligera* Marion & Bobretzky, 1875 (*A*) anterior end, dorsal view; (*B*) prostomium and anteriormost segments, ventral view; (*C*) pharyngeal armature; (*D*) compound chaetae, anterior parapodia; (*E*) aciculae, anterior parapodia; (*F*) compound chaetae, midbody; (*G*) compound chaetae, posterior parapodia; (*H*) acicula, posterior parapodia; (*I*) dorsal simple chaeta; (*J*) ventral simple chaeta. AM W28416. Scales: *A* 0.4 mm, *B* 0.18 mm, *C* 0.1 mm, *D–J* 20 μm.

33°33'S 151°14'E, A. Jones & party, 16 May 1980, 1 (AM W196609); E end of Brooklyn Boat Channel, Hawkesbury R., 33°33'S 151°14'E, coll. A. Jones *et al.*, 1 Aug 1979, 2 (AM W196611); E end of Brooklyn Boat Channel, Hawkesbury R., 33°33'S 151°14'E, coll. A. Jones *et al.*, 18 Dec 1979, 1 (AM W196612); E end of Brooklyn Boat Channel, Hawkesbury R., 33°33'S 151°14'E, coll. A. Jones & party, 18 Dec 1979, 1 (AM W196613); Barrenjoey Head, Broken Bay, 33°35'S 151°20'E, algae on rocky substrate, 4 m, coll. J.K. Lowry & party 22 Apr 1983, 1 (AM W28408). WESTERN AUSTRALIA: N end of beach, Bundegi Reef, Exmouth Gulf, 21°49'S 114°11'E, rocky rubble, sticky sediment & brown algae with epiphytes, 2 m, coll. H.E. Stoddart, 4 Jan 1984, many + 2 on SEM stub (AM W28952); N end of beach, Bundegi Reef, Exmouth Gulf, 21°49'S 114°11'E, rocky rubble, coralline algae with green epiphyte, 1.5 m, coll. H.E. Stoddart, 4 Jan 1984, several (AM W28953).

Description. Body up to 4.5 mm long, 0.3 mm wide, with 40 chaetigers, slightly dorsoventrally flattened, dorsally convex along median line of body, with well marked segments. Distinct colour pattern, with 1 transverse band of red pigment, sometimes 2 bands, and additional narrow bands often laterally located on posterior half of segments (Fig. 13A). Material examined exhibiting great variation in intensity of pigmentation, from highly pigmented to colourless individuals. Prostomium twice as large as 2nd segment, pentagonal to quadrangular, with nuchal notch, ciliated on both sides (Fig. 13A), double semicircle of cilia on anterior part of prostomium (Fig. 12D,E); 4 eyes in open trapezoidal arrangement, occasionally 2 anterior eyespots. Antennae, tentacular and dorsal cirri fusiform, smooth. Lateral antennae arising in front of anterior eyes, length similar to combined length of prostomium and palps, median

antenna typically much longer than lateral antennae, arising slightly posteriorly to lateral antennae (Figs 12D,E, 13A). Palps broad (Fig. 12F), shorter than prostomium. Peristomium shorter than following segments, sometimes covered partially by prostomium and fold of chaetiger 1, provided with some cilia (Figs 12D,E, 13A); dorsal tentacular cirri shorter than median antenna but longer than lateral antennae; ventral tentacular cirri similar to lateral antennae. Dorsal transverse row of cilia on each segment (Figs 12D, 14A); plus some cilia on dorsal surface of parapodial lobes (Fig. 14A). Dorsal cirri of chaetiger 1 long, similar in length to median antenna, longer than body width; remaining dorsal cirri irregularly alternating between cirri similar in length to half of body width, and cirri much shorter (Figs 12D, 13A, 14A). Parapodia short, about third of body width, thick, conical. Ventral cirri broad, shorter than parapodial lobes or similar in length (Figs 13G, 14A). Compound chaetae heterogomph falcigers, shafts with several thin subdistal spines; blades proportionally short, unidentate, with rounded tips, and short spines on margin (Fig. 13B,C). Anterior parapodia with 2 kinds of compound chaetae, one with relatively thin blades, 3 in anterior segments, declining to 1 from midbody onwards (Figs 13B, 14C), blades 20–25 µm in length, located dorsally, other type with thicker and shorter blades (Figs 13C, 14D,E), about 17 µm in length, all similar, 12–14 per parapodium. Dorsal simple chaetae bayonet-shaped (Figs 13D, 14B), from proventricle segments onwards. Ventral simple chaetae absent. Acicula solitary, distally knobbed, apparently hollow at tip (Fig. 13E). Pharynx through 4–5 segments; opening rim smooth on one half and other half with small denticles (Figs 13A,F); material examined exhibiting considerably range in numbers of denticles present, from few to 20–24. Pharyngeal tooth large, conical to rhomboidal; pharyngeal opening provided with crown of about 14 soft papillae (Fig. 13F). Proventricle longer than pharynx, through 7–8 segments, with about 50 muscle cell rows. Pygidium with 2 slender, anal cirri.

Remark. Material from all localities listed in the distribution has been examined by the senior author during other studies, and no morphological differences between them can be found. Molecular studies may be useful to confirm if this is a widely distributed species or a suite of sibling species. Specimens described as *Eusyllis autolytoides* by Hartmann-Schröder (1991) and *Odontosyllis multidentata* (Hartmann-Schröder, 1982) agree with the description of *Eusyllis kupfferi*, so we consider them as synonymous.

Distribution. Portugal (Madeira), Canary Is., Cuba, Australia (Queensland, Western Australia, New South Wales).

Habitat. Occurring on hydroids, *Rhizophora mangle* roots, on algae, algae with sand, debris, dead corals, sand and mud, from intertidal to about 20 m.

Eusyllis lamelligera Marion & Bobretzky, 1875

Figs 15A–J, 16A–F

Eusyllis lamelligera Marion & Bobretzky, 1875: 33, pl. 3, figs. 9A–C.—Fauvel, 1923: 294, Fig. 113.—San Martín, 2003: 117, figs 54, 55.
Eusyllis dentata Hartmann-Schröder, 1990: 50, figs 13–16.
Eusyllis habei Imajima, 1966: 97, text-fig. 31a–k.

Material examined. AUSTRALIA: NEW SOUTH WALES: N side of Bannister Head, N of Ulladulla, 35°19.15'S 150°29.12'E, grey sponge from top of boulder, 18 m, coll. K. Attwood, 6 May 1997, 1 (AM W28960); SW of Bowen Is., Jervis Bay, 35°07.49'S 150°45.77'E, small white sponge with pink lobes, from seagrass bed, 7 m, coll. P. Serov & G.D.F. Wilson, 8 Dec 1993, several (AM W28416); SW of Bowen Is., Jervis Bay, 35°07.49'S 150°45.77'E, rock on sandy bottom covered in bryozoa & polychaetes, 7 m, coll. P. Serov & G.D.F. Wilson, 8 Dec 1993, few (AM W28415); Montagu Roadstead, Jervis Bay, 35°02.2'S 150°46.0'E, unvegetated sediment, 12 m, coll. P.A. Hutchings & party, 6 Jun 1990, 1 (AM W28231); NW corner of Bowen Is., Jervis Bay, 35°06.81'S 150°46.11'E, dense bryozoans under rock ledge, 13 m, coll. P. Serov & G.D.F. Wilson, 8 Dec 1993, several (AM W28959); Darling Road, near anchorages, Jervis Bay, 35°7.3'S 150°44.1'E, 18 m, coll. P.A. Hutchings, 23 Jan 1973, 2 (AM W28437); Taupo Seamount, Tasman Sea, 33°16.85'S 156°09.15'E, limestone & sand bottom, 244 m, coll. J.K. Lowry & party, on RV "Franklin", 2 May 1989, 5 on SEM stub (AM W28877); Taupo Seamount, Tasman Sea, 33°16.85'S 156°09.15'E, limestone & sand bottom, 244 m, coll. J.K. Lowry & party on RV "Franklin", 2 May 1989, many (AM W28927); Reef flat, near wreck "Yoshin Maru Iwaki", Elizabeth Reef, Tasman Sea, 29°55.8'S 159°01.3'E, algae, 0.5 m, coll. Elizabeth & Middleton Reefs Expedition, 1987, 14 Dec 1987, several (AM W28928). TASMANIA: Woodchip Jetty, Spring Bay, Triabunna, 42°30'S 147°55'E, muddy bottom, 4 m, coll. D. Cropp, Nov 1982, 1 (AM W199178). SOUTH AUSTRALIA: Billy Lights Point, Port Lincoln, 34°45'S 135°53'E, stone washings from sheltered intertidal rocks, coll. I. Loch, 15 Feb 1985, 1 (AM W28929). WESTERN AUSTRALIA: Goss Passage, Beacon Is. 28°25.5'S 113°47'E, dead plates of *Acropora* coral covered in coralline algae, 24 m, P.A. Hutchings, 21 May 1994, 1 (AM W28374); N end of Long Is. 28°27.9'S 113°46.3'E, dead coral substrate covered in coralline & brown algae, 5.5 m, coll. C. Bryce, 22 May 1994, several (AM W28961).

Additional material examined *Eusyllis dentata* AUSTRALIA: NEW SOUTH WALES: Angourie Point, south of Yamba, 29°29'S 153°22'E algae, intertidal, holotype (HZM P-19963), 8 paratypes (HZM P-19964), 1 (HZM P-203313). *Eusyllis habei* JAPAN: Bos Peninsula, Hubara Port, 1, coll. E. Nishi. *Eusyllis lamelligera* SPAIN: off Punta Jovo, W. W Menorca, Balearic Is. 10 m, algae 43°40.27'–43°40.06'N 5°13.36'–5°14.35'E, 6 (MNCNM 8675); NW Cabo de Lastres, Asturias, Cantabrian Sea, NE Atlantic, 39°49.66'–39°47.64'N 2°40.78'–2°38.71'E, 146 m, 8 (MNCNM 8688).

Description. Complete specimen 6.3 mm long, 0.5 mm wide, with 50 chaetigers. Prostomium semi-circular; 4 eyes in open trapezoidal arrangement and 2 anterior eyespots. Median antenna more than twice combined length of prostomium and palps, inserted on middle of prostomium, lateral antennae shorter than median antenna, inserted in front of anterior eyes, near anterior margin (Fig. 15A). Palps broad, similar in length to prostomium (Fig. 15A). Nuchal organs with distinct ciliation, extending to posterior margin of prostomium (Figs 15A, 16A). Peristomium similar to subsequent segments; dorsal tentacular cirri long and slender, more than twice as long as body width, ventral tentacular cirri about third length of dorsal cirri. Antennae, tentacular and dorsal cirri smooth, long, slender, distally tapered (Fig. 15A), sometimes rugose to weakly pseudo-articulate (Fig. 16B). Dorsal cirri of chaetiger 1 longer than dorsal tentacular cirri, remaining dorsal cirri irregularly alternating long, and short cirri, long cirri much longer than body width, and short ones, slightly shorter than body width (Fig. 15A). Ventral cirri of chaetiger 1 enlarged, flattened leaf-like; following ones conical (Figs 15B, 16B); ventral cirri with minute pores (Fig. 16D). Lateral tufts of cilia on each segment (Fig. 16C). Compound chaetae heterogomph, with subdistal spines on shafts and bidentate blades, both teeth similar in size, well separated and rounded margin between both teeth, and fine spines on margin (Figs. 15D,F,G, 16E,F). Anterior parapodia with about 20–25 compound chaetae, with strong dorsoventral gradation in

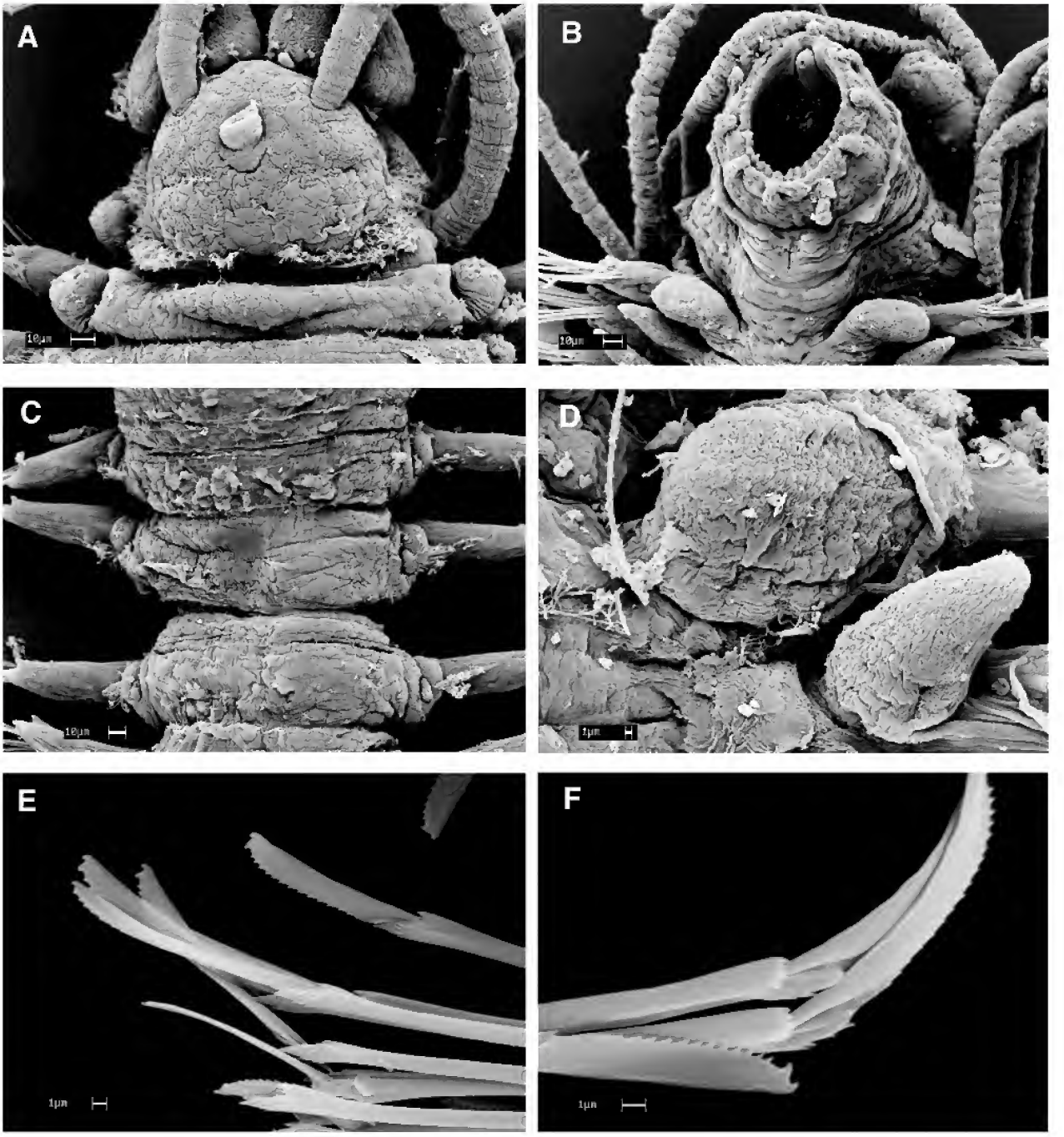


Fig. 16. SEM of *Eusyllis lamelligera* Marion & Bobretzky, 1875 (*A*) prostomium; (*B*) everted pharynx and anteriormost segments, ventral view; (*C*) midbody segments, dorsal view; (*D*) detail of first and second ventral cirri; (*E,F*), compound chaetae. AM W28877

size of blades within fascicle, about 40 µm in length dorsally, 21 µm in length ventrally. Progressively along body, number of compound chaetae per parapodium decreases, to 13–15 on midbody, 10 on posterior parapodia, with thicker shafts and blades, with less marked dorsoventral gradation in length of blades; on midbody, blades about 35 µm in length dorsally, 22 µm in length ventrally, and 30 µm in length dorsally, and 15 µm in length ventrally on posterior parapodia (Fig. 15D,F,G). Dorsal simple chaetae on posterior parapodia, slender, bidentate, both teeth similar, with short spines on margin (Fig. 15I). Ventral simple chaetae on far posterior parapodia, similar to dorsal simple chaetae, but larger and teeth well separated (Fig. 15J). Anterior parapodia with 2 aciculae, one distally knobbed with acute tip, other with tricuspid tip, with lateral ones poorly developed (Fig. 15E); medium and posterior parapodia each with single acicula, distinctly tricuspid (Fig. 15H). Pharynx through about 7 segments; pharyngeal tooth, conical, on anterior margin; trepan variable, ranging from few small teeth present to distinct incomplete crown of up to 24 teeth (Figs 15C, 16B).

Remarks. This species is characterized by having enlarged, flattened leaf-like ventral cirri on chaetiger 1, tricuspid aciculae, and compound chaetae with bidentate blades, with both teeth of similar size and well separated by rounded

margin. The Australian specimens were described as *Eusyllis dentata* by Hartmann-Schröder (1990); and these were examined and they are indistinguishable from Mediterranean specimens of *Eusyllis lamelligera*. This species has been reported from a wide range of habitats and depths and material should be re-examined and a molecular study would be useful to confirm if this is a widely distributed species or a suite of sibling species.

Eusyllis habei Imajima, 1966, from Japan, is also similar according to the description and may represent the same species according to Imajima (1966). The material examined from Bos Peninsula, Japan appears to be similar to specimens of *E. lamelligera* from the Mediterranean and also to material from the Atlantic and Australia.

Habitat. Occurring in a wide variety of substrates and depths, intertidally to depths greater than 500 m.

Distribution. North Atlantic, Mediterranean Sea, Australia (New South Wales, Tasmania, Western Australia).

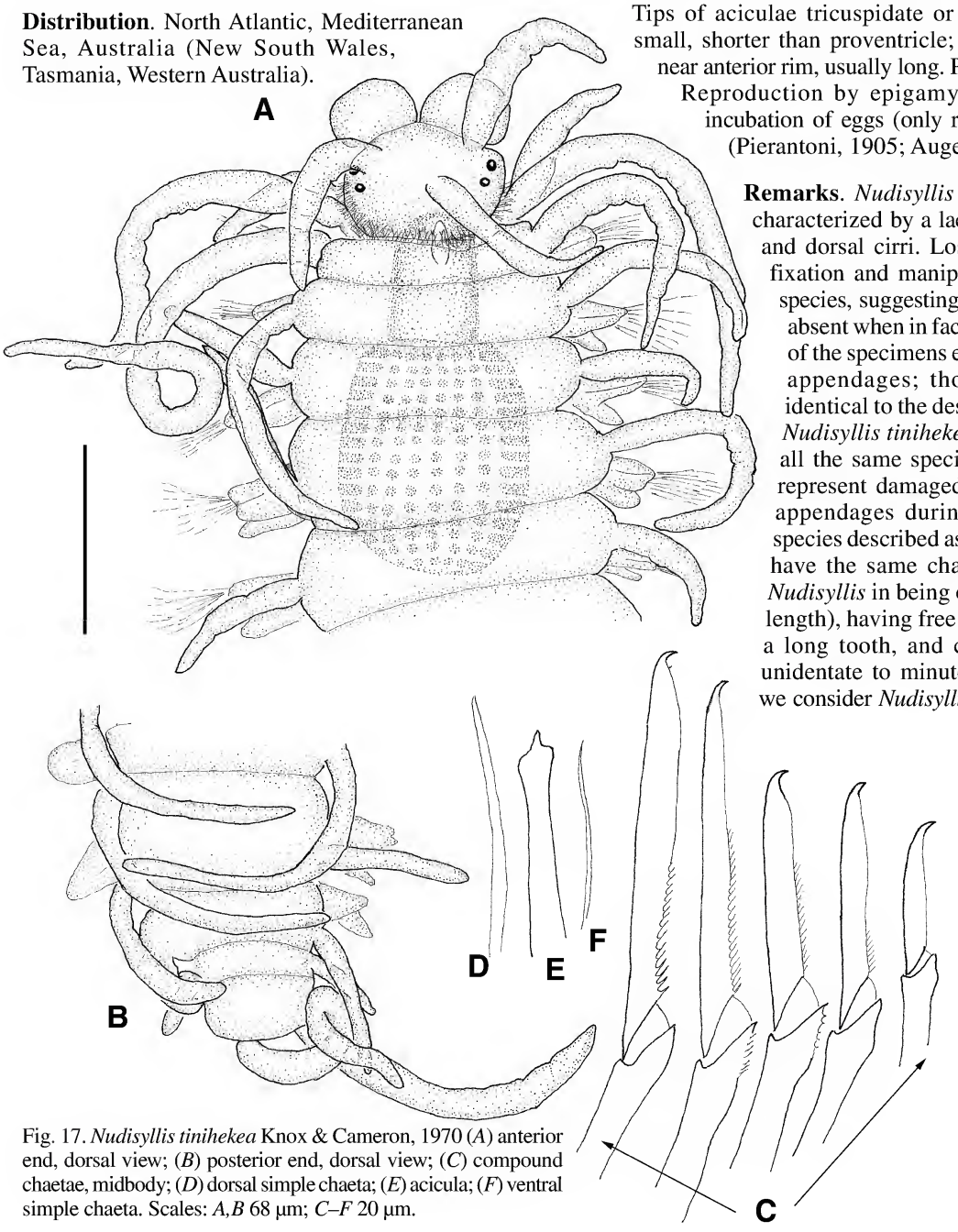


Fig. 17. *Nudisyllis tinihekea* Knox & Cameron, 1970 (*A*) anterior end, dorsal view; (*B*) posterior end, dorsal view; (*C*) compound chaetae, midbody; (*D*) dorsal simple chaeta; (*E*) acicula; (*F*) ventral simple chaeta. Scales: *A,B* 68 µm; *C–F* 20 µm.

Genus *Nudisyllis* Knox & Cameron, 1970

Nudisyllis Knox & Cameron, 1970: 77, emended.

Type species. *Nudisyllis tinihekea* Knox & Cameron, 1970.

Diagnosis. Body small, fragile, <5 mm in length. Prostomium large, about width of 2 segments, with 4 eyes and sometimes pair of anterior eyespots. Three antennae. Palps separated, free from each other, sometimes adjacent at base. Median antenna inserted on middle of prostomium or anteriorly, on line with lateral antennae. Two pairs of tentacular cirri. Nuchal organs as 2 ciliated grooves between prostomium and peristomium. Dorsal cirri on all chaetigers, long, cylindrical, smooth or slightly rugose. Ventral cirri not modified. Compound chaetae with both unidentate and bidentate blades on same parapodium, or all unidentate; bidentate blades having proximal tooth small, spine-like. Tips of aciculae tricuspidate or lancet-shaped. Pharynx small, shorter than proventricle; pharyngeal tooth located near anterior rim, usually long. Pygidium with 2 anal cirri. Reproduction by epigamy, probably with dorsal incubation of eggs (only reported on two species) (Pierantoni, 1905; Augener, 1913).

Remarks. *Nudisyllis* was described as being characterized by a lack of antennae, tentacular and dorsal cirri. Loss of appendages during fixation and manipulation is usual in some species, suggesting that these structures are absent when in fact they are present. Several of the specimens examined lack all or some appendages; those that lack them are identical to the description and drawings of *Nudisyllis tinihekea*, so we assume that are all the same species; they type specimens represent damaged specimens, having lost appendages during fixation. Some other species described as belonging to *Pionosyllis* have the same characters, but differ from *Nudisyllis* in being of minute size (<5 mm in length), having free palps, short pharynx and a long tooth, and compound chaetae with unidentate to minutely bidentate blades. So, we consider *Nudisyllis* a valid genus, and have

emended the diagnosis and the genus now includes some species previously considered belonging to *Pionosyllis*, among them *P. pulligera* (Krohn, 1852); *P. magnidens* Day, 1953; and *P. divaricata* (Keferstein, 1862).

Nudisyllis tinihekea Knox & Cameron, 1970

Fig. 17A–F

Nudisyllis tinihekea Knox & Cameron, 1970: 77, figs 6–9.
Pionosyllis pulligera.—Augener, 1913: 221, pl. II, fig. 8, text-fig. 29. Not Krohn, 1852: 251.
Pionosyllis samsonensis Hartmann-Schröder, 1980: 52, figs 39–43; 1981: 32; 1982: 65. 1983: 130; 1984: 20; 1985: 69; 1986: 41; 1987: 38; 1991: 35.

Material examined. AUSTRALIA: NEW SOUTH WALES: Barrenjoey Head, Broken Bay, 33°35'S 151°20'E, algae on rocky substrate, 4 m, coll. J.K. Lowry & party 22 Apr 1983, 1 (AM W28966). WESTERN AUSTRALIA: Red Bluff, Kalbarri, 27°42'S 114°09'E, seagrass in shallow sand on rocky shore, 3.5 m, coll. R.T. Springthorpe, 10 Jan 1984, 2 (AM W28968); Red Bluff, Kalbarri, 27°42'S 114°09'E, mixed coralline algae on rocky shore, 3.5 m, coll. J.K. Lowry, 10 Jan 1984, several (AM W28970); Inshore limestone reef, Ned's Camp, Cape Range National Park, 21°59'S 113°55'E, frilly *Caulerpa* sp., 1 m, coll. J.K. Lowry, 2 Jan 1984, several (AM W28971); Inside outer Ningaloo Reef, Cape Range National Park, 21°59.5'S 113°54.5'E, mixed algae, 2 m, coll. J.K. Lowry, 1 Jan 1984, 2 (AM W28364); Inshore limestone reef, Ned's Camp, Cape Range National Park, 21°59'S 113°55'E, sponge covered with epiphytes, sediment & muddy worm tubes, 1.5 m, coll. R.T. Springthorpe, 2 Jan 1984, 2 (AM W28969); N end of beach, Bundegi Reef, Exmouth Gulf, 21°49'S 114°11'E, rocky rubble, coralline algae with green epiphyte, 1.5 m, coll. H.E. Stoddart, 4 Jan 1984, 1 (AM W28967).

Description. Body up to 3.1 mm long with 34 chaetigers, according to literature, longest specimen examined 1.2 mm long, 0.2 mm wide, with 16 chaetigers, extremely fragile, several specimens lack most appendages, others having lost all antennae, tentacular and dorsal cirri. Prostomium squared to pentagonal, densely covered by long cilia on posterior margin and laterals (Fig. 17A), 4 eyes in trapezoidal arrangement, located laterally on prostomium; median antenna inserted on middle of prostomium, fusiform, distally tapered, slightly longer than combined length of prostomium and palps; lateral antennae inserted on anterior margin, slightly shorter than median antenna (Fig. 17A). Palps short, broad, oval. Peristomium dorsally reduced, covered by chaetiger 1 (Fig. 17A); dorsal tentacular cirri long, about twice as long as median antenna; ventral tentacular cirri about one third length of dorsal ones. Dorsal cirri smooth, thick, distally tapered, long on anterior segments, from proventricle posteriorly, cirri consist of long and short cirri that alternate; long cirri longer than body width, and short cirri, shorter than body width (Fig. 17A). Parapodia conical, ending with rounded papilla, provided with some tufts of cilia. Ventral cirri digitiform, shorter than parapodial lobes. Compound chaetae similar throughout, 15 anteriorly, 7 posteriorly, blades elongated, distally slightly hooked, unidentate, longer ones with subdistal spine, smooth or provided with fine spines on margin (Fig. 17C); dorsoventral gradation in length within fascicle, about 42 µm in length dorsally, 15 µm in length ventrally. Dorsal and ventral simple chaetae on far posterior parapodia, slender, smooth, unidentate (Fig. 17D,F). Acicula solitary, with tricuspidate tip (Fig. 17E). Pharynx short, through 2 segments; single pharyngeal tooth on anterior margin (Fig. 17A). Proventricle barrel-shaped, through 3 segments, with about 20 muscle cell rows. Pygidium semi-circular, with 2 anal cirri, similar in shape and length to long dorsal cirri (Fig. 17B).

Habitat. Occurring on coralline algae, mixed algae, *Caulerpa*, seagrasses on sand, sand with debris, sponges with epibionts in shallow depths.

Distribution. New Zealand, Australia (New South Wales, Western Australia, South Australia, Victoria, Queensland).

Genus *Odontosyllis* Claparède, 1863

Odontosyllis Claparède, 1863: 47.
?*Eurymedusa* Kinberg, 1865: 61.
Parautolytus Ehlers, 1900: 213.
?*Alluaudella* Gravier, 1905: 372.
?*Atelesyllis* Pruvot, 1930: 39.
Pharyngeovalvata Day, 1951: 26.
Odontoautolytus Hartmann-Schröder, 1979: 112.
?*Synpalposyllis* Hartmann-Schröder, 1983: 132.
Umbellisyllis Sars, 1869: 254.

Type species. *Syllis fulgurans* Audouin & Milne Edwards, 1833, designated by Hartman, 1959.

Diagnosis. Body of variable size, from <5 mm to >10 mm in length, with numerous segments, cylindrical, dorsally highly convex, flattened ventrally. Prostomium with 4 eyes and, sometimes, pair of anterior eyespots. Three antennae. Palps broad, free for almost all their length, fused basally. Peristomium usually reduced dorsally; 2 pairs of tentacular cirri. Occipital flap present, usually well developed, covering peristomium dorsally and prostomium partially. Nuchal organs as 2 ciliated grooves between prostomium and peristomium, extending sometimes to lateral areas of prostomium. Dorsal cirri elongated, smooth, distally tapered, but sometimes short or indistinctly articulated. Parapodia usually with pre- and postchaetal lobes. Ventral cirri digitiform to pillow-shaped. Compound chaetae heterogomph, usually with shafts distally spinose. Dorsal and ventral simple chaetae present on some parapodia. Pharynx short, distinctly shorter than proventricle, provided with several teeth, usually few, pointing backwards, pharyngeal mid-dorsal tooth absent; pharynx when not everted situated posteriorly to chaetiger 1, inside tube that leads to mouth opening on peristomium. Proventricle usually long and wide, massive. Pygidium with 2 anal cirri. Reproduction by epigamy; epigamic specimens sometimes strongly modified and phosphorescent (Fischer & Fischer, 1995; Gaston & Hall, 2000).

Remarks. The structure of the anterior part of the gut in this genus is distinct and unusual, with the pharynx being short and the opening located posteriorly to the mouth; a tube is present that surrounds the pharynx and that leads to the mouth. This must be removed to see the trepan and the two lateral plates of the pharynx. Occasionally specimens lack any teeth on the trepan, and we suggest that individuals can regenerate these teeth. The genera that we have synonymized with *Odontosyllis* have been inadequately examined previously with regard to the structure of the anterior part of the gut. For example, GSM examined one paratype of *Pharyngeovalvata natalensis* (BMNH 1961.16.16-17, Natal Shore, South Africa Stn. 47.8, coll: J.H. Day) and it is identical to specimens of *Odontosyllis ctenostoma* Claparède, 1868. Both species possess a pharynx with a trepan; even though the description of the

pharynx of *Pharyngeovalvata* by Day (1951) states that the pharynx lacks a trepan, the paratype possesses one. We therefore have synonymized these two species that are the type species of their respective genera and *Pharyngeovalvata* is synonymized with *Odontosyllis*. We suspect that *Atelesyllis* Pruvot, 1930, is also identical to *Odontosyllis* with the pharynx contracted, but the types appear to be lost. We have also examined the holotype of *Synpalposyllis australiensis* Hartmann-Schröder, 1983 (HZM P-17400), a species known only from the holotype, which is less than 5 mm in length, with the prostomium and the anterior part of the pharynx damaged so it is not possible to verify the presence or absence of the palps, but the chaetae and aciculae are similar to those of *O. australiensis*. In our opinion, this specimen may be a juvenile of *O. australiensis*. Types of *Alluaudella madagascariensis* Gravier, 1905 were not available for examination but this species appears to be related to some species of *Odontosyllis* with short dorsal cirri and indistinct ventral cirri, distally located, and partially fused, appearing as absent, although this should be checked on material from the type locality. We have examined type material of the other species of the genus, *Alluaudella longicirrata* Mohammad, 1973, and it is clearly a species of *Odontosyllis*. We suggest that it is likely that the genus *Alluaudella* should be synonymized with *Odontosyllis*, and it certainly does not belong in the subfamily Autolytinae where it has previously been placed (Gravier, 1905).

The key below includes nine species, an additional two species have been reported from Australia, but they are not included in the key. *Odontosyllis hyalina* Grube, 1878, was reported by Hartmann-Schröder (1990); and we have examined the specimen (HZM P-20185) and it is a small, probably a juvenile specimen, belonging to *O. australiensis*; the original description (Grube, 1878) is based on a single, epigamic specimen (MPUW, 325), in poor condition, but the compound chaetae are similar to those of *O. australiensis* but the shafts are proportionally larger, the blades are shorter, some of them almost unidentate. Haswell (1920) reported two specimens of *Odontosyllis suteri* Benham, 1915, from Port Jackson, Sydney, as the type description from New Zealand specimens is incomplete and no details of the chaetae are given it is therefore difficult to verify Haswell's identification, and we suggest that they may represent individuals of *Odontosyllis polycera*. So neither of these records of *O. hyalina* and *O. suteri* from Australia are likely to be valid.

Key to Australian species of *Odontosyllis*

1 Occipital flap present (Fig. 32A) 2
—— Occipital flap absent or indistinct (Fig. 18A) 6

2 Occipital flap totally covering prostomium and palps ..... *O. marombibooral* n.sp.
—— Occipital flap covering only posterior part of prostomium 3

3 Antennae, tentacular and dorsal cirri ovoid, globular, or sphaerical (Fig. 26A) ..... *O. globulocirrata*
—— Antennae and cirri elongate, not as above 4

4 Dorsal cirri short, slightly longer than parapodial lobes. Blades of compound chaetae elongated, unidentate. Parapodial lobes elongated and distinctly bifid (Fig. 24C) ..... *O. freycinetensis*
—— Dorsal cirri long, filiform, distinctly longer than parapodial lobes Fig. 35A). Compound chaetae either bidentate or bidentate plus unidentate. Parapodial lobes not elongated 5

5 Large size (up to 25 mm long). Occipital flap covering almost all prostomium, reaching to level of base of antennae (Fig. 35A). Ventral cirri pillow-shaped ..... *O. polycera*
—— Medium size (up to 6.6 mm long). Occipital flap covering only posterior part of prostomium (Fig. 20A). Ventral cirri ovoid ..... *O. australiensis*

6 Dorsal cirri ovoid, shorter than parapodial lobes or similar in length. Ventral cirri distally inserted ..... *O. annulatus*
—— Dorsal cirri elongated, distinctly longer than parapodial lobes. Ventral cirri inserted basally on parapodial lobes 7

7 Compound chaetae claw-shaped, unidentate or indistinctly bidentate (Fig. 22C) ..... *O. detecta*
—— Compound chaetae with some elongated blades, some distinctly bidentate 8

8 Blades of compound chaetae mostly unidentate, and some bidentate. Dorsum with dark transverse bands or without colour markings ..... *O. langerhansiaesetosa*
—— All blades bidentate. Dorsum with 3 longitudinal dark rows ..... *O. gravelyi*

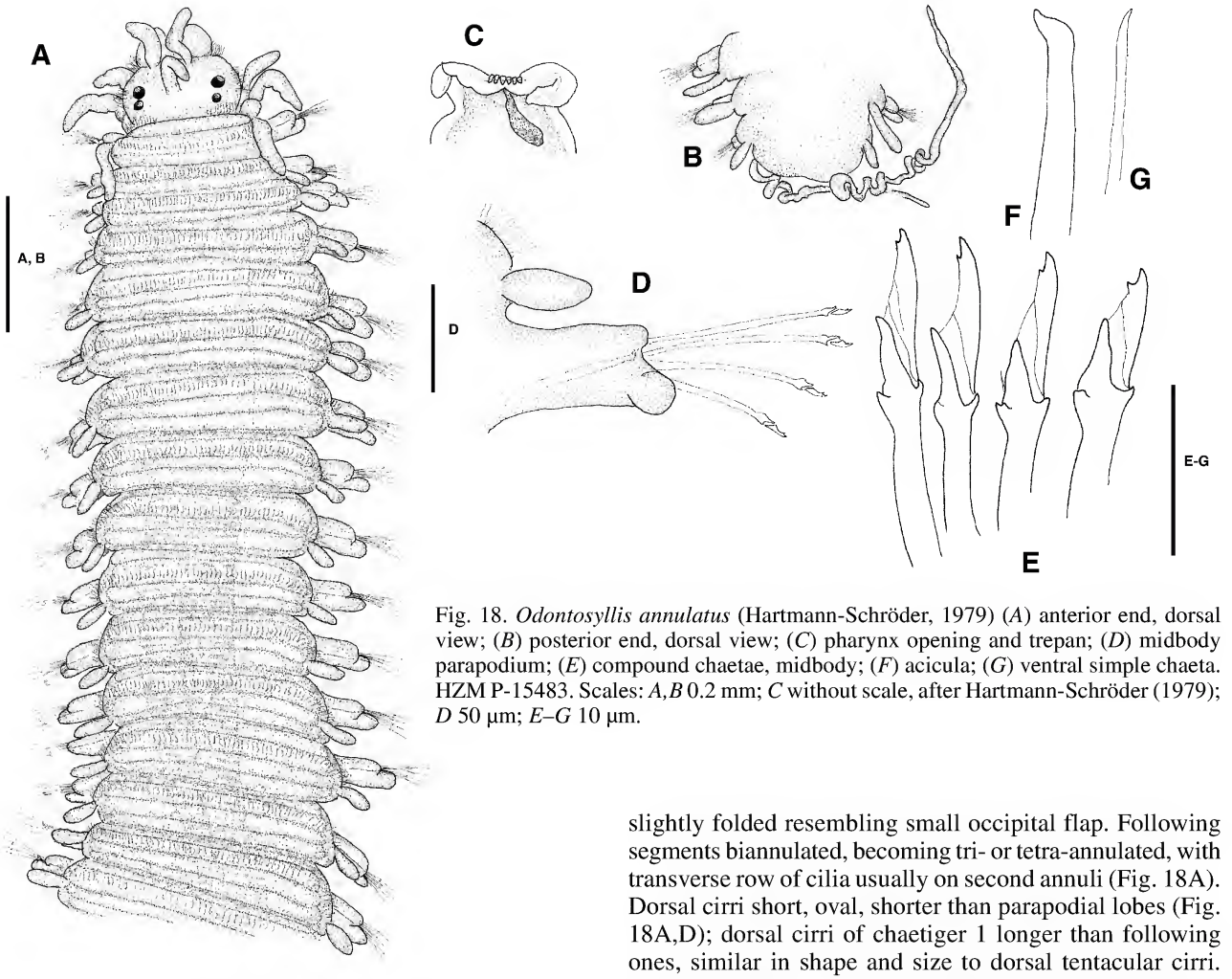


Fig. 18. *Odontosyllis annulatus* (Hartmann-Schröder, 1979) (*A*) anterior end, dorsal view; (*B*) posterior end, dorsal view; (*C*) pharynx opening and trepan; (*D*) midbody parapodium; (*E*) compound chaetae, midbody; (*F*) acicula; (*G*) ventral simple chaeta. HZM P-15483. Scales: *A,B* 0.2 mm; *C* without scale, after Hartmann-Schröder (1979); *D* 50 µm; *E–G* 10 µm.

Odontosyllis annulatus (Hartmann-Schröder, 1979)

Fig. 18A–G

Odontoautolytus annulatus Hartmann-Schröder, 1979: 112, figs 178–182.
Odontosyllis brevicirra Hartmann-Schröder, 1991: 34, figs 54–56.

Material examined. AUSTRALIA: WESTERN AUSTRALIA: Port Hedland, 19°38'S 119°31'E, coarse sediments, intertidal, 28 Sept. 1975, holotype of *Odontoautolytus annulatus* (ZMH P-15482) and 2 paratypes (ZMH P-15483). QUEENSLAND: Gladstone, 23°49'S 151°25'E, coarse sand, 28 Jan 1976, holotype of *Odontosyllis brevicirra* (HZM P-20543) and 1 paratype (HZM P-20544). All material collected Hartmann-Schröder.

Description. Body long, slender, (Fig. 18A), about 4.8 mm long, 0.3 mm wide, with 47 chaetigers. Prostomium oval, laterally convex, with 2 lateral and 2 frontal tufts of cilia (Fig. 18A); 4 eyes in rectangular arrangement, those of anterior pair slightly larger than posterior ones; antennae short, digitiform, shorter than prostomium; median antenna inserted between anterior eyes; lateral antennae inserted near anterior margin, close to each other, near midline of margin (Fig. 18A). Palps shorter than prostomium, blunt. Peristomium shorter than subsequent segments; tentacular cirri similar to antennae; dorsal ones longer than ventral ones. Occipital flap absent, although some with peristomium slightly folded resembling small occipital flap. Following segments biannulated, becoming tri- or tetra-annulated, with transverse row of cilia usually on second annuli (Fig. 18A). Dorsal cirri short, oval, shorter than parapodial lobes (Fig. 18A,D); dorsal cirri of chaetiger 1 longer than following ones, similar in shape and size to dorsal tentacular cirri. Ventral cirri fused with parapodial lobes, inserted distally (Fig. 18A,D). Parapodia each with 4 compound chaetae (Fig. 18D), strongly heterogomph, shafts with subdistal large tooth, and short, smooth, triangular, bidentate blades, subdistal tooth small, all similar in shape and length (Fig. 18E), 7–8 µm in length. Solitary ventral simple chaeta on far posterior parapodia of one specimen, slender, smooth, unidentate (Fig. 18G). Dorsal simple chaetae not observed. Solitary acicula on each parapodium, distally acuminate (Fig. 18F). Pygidium large, slightly bilobed, with 2 long, slender, filiform anal cirri (Fig. 18B). Pharynx through about 2 segments, according to original description, trepan with 6 small teeth (Fig. 18C); dark gland near pharynx opening (Fig. 18C). Proventricle long and slender, through about 7–8 segments (Fig. 18A), with about 50 muscle cell rows.

Remarks. This species has small ventral cirri, inserted distally. Hartmann-Schröder (1979) made an incorrect interpretation of the parapodia, overlooked the ventral cirri and described it as a new genus, which she placed in the subfamily Autolytinae. Nygren (2004) synonymized *Odontoautolytus* with *Odontosyllis*. After examination of the type series of both species, *Odontoautolytus annulatus* and *Odontosyllis brevicirra*, we suggest that they represent the same species *Odontosyllis annulatus*.

Habitat. Occurring in coarse sediments, intertidally.

Distribution. Australia (Western Australia, Queensland).

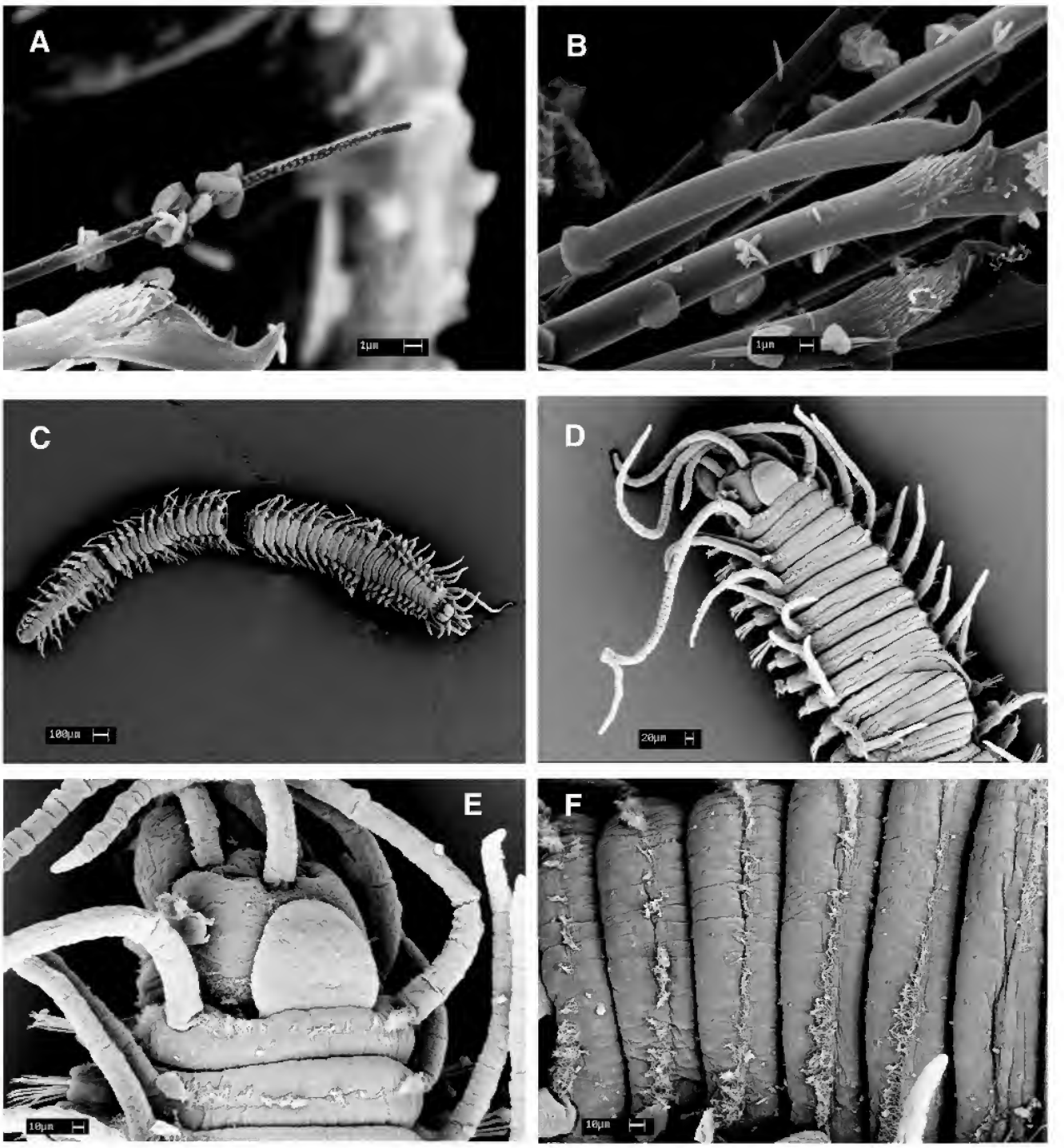


Fig. 19. SEM of *Odontosyllis polycera* Schmarda, 1863 (*A*) dorsal simple chaeta; (*B*) ventral simple chaeta. SEM of *Odontosyllis australiensis* Hartmann-Schröder, 1979 (*C*) complete specimen, ventral view; (*D*) anterior end, dorsal view; (*E*) prostomium and anteriormost segments; (*F*) midbody segments, lateral view. *A,B*: AM W4344; *C–F*: AM W28380.

Odontosyllis australiensis Hartmann-Schröder, 1979

Figs 19C–F, 20A–H, 21A–F

Odontosyllis australiensis Hartmann-Schröder, 1979: 95, figs 97–104; 1981: 31; 1984: 20.

?*Odontosyllis hyalina*.—Hartmann-Schröder, 1990: 50. Not Grube, 1878: 129.

Odontosyllis fulgurans.—Haswell, 1920: 107. Not Audouin & Milne Edwards, 1834: 229.

Synpalposyllis australiensis Hartmann-Schröder, 1983: 132, figs 18–20.

Material examined. AUSTRALIA: NEW SOUTH WALES: 100 m NW of Julian Rocks, Byron Bay, 28°36.8'S 15°37.8'E, shell and gravel, 15 m, coll. Ho & party, 3 Mar 1992, 1 (AM W28217). WESTERN AUSTRALIA: N end of Long Is., 28°27.9'S 113°46.3'E, dead coral substrate covered in coralline & brown algae, 5.5 m, coll. C. Bryce, 22 May 1994, 2 on SEM stub, (AM W28380); Lafontaine Is., Kimberley region, 14°10'S 125°47'E, 15m, coll P.A. Hutchings, 19 July 1988, 1 (AM W28933); Reef south of Lucas Is., Brunswick Bay, Kimberley region, 15°16'S 124°29'E, 2 m, coll P.A. Hutchings, 24 July 1988, 1 (AM W28932).

Additional material. AUSTRALIA: WESTERN AUSTRALIA. Denmark, Ocean Beach, algae, 18 Nov. 1975, coll. & id. Hartmann-Schröder, holotype of *Synpalposyllis australiensis*, (HZM P-17400). Singapore, syntype of *Odontosyllis hyalina* Grube, 1878: 129, (MPUW 325).

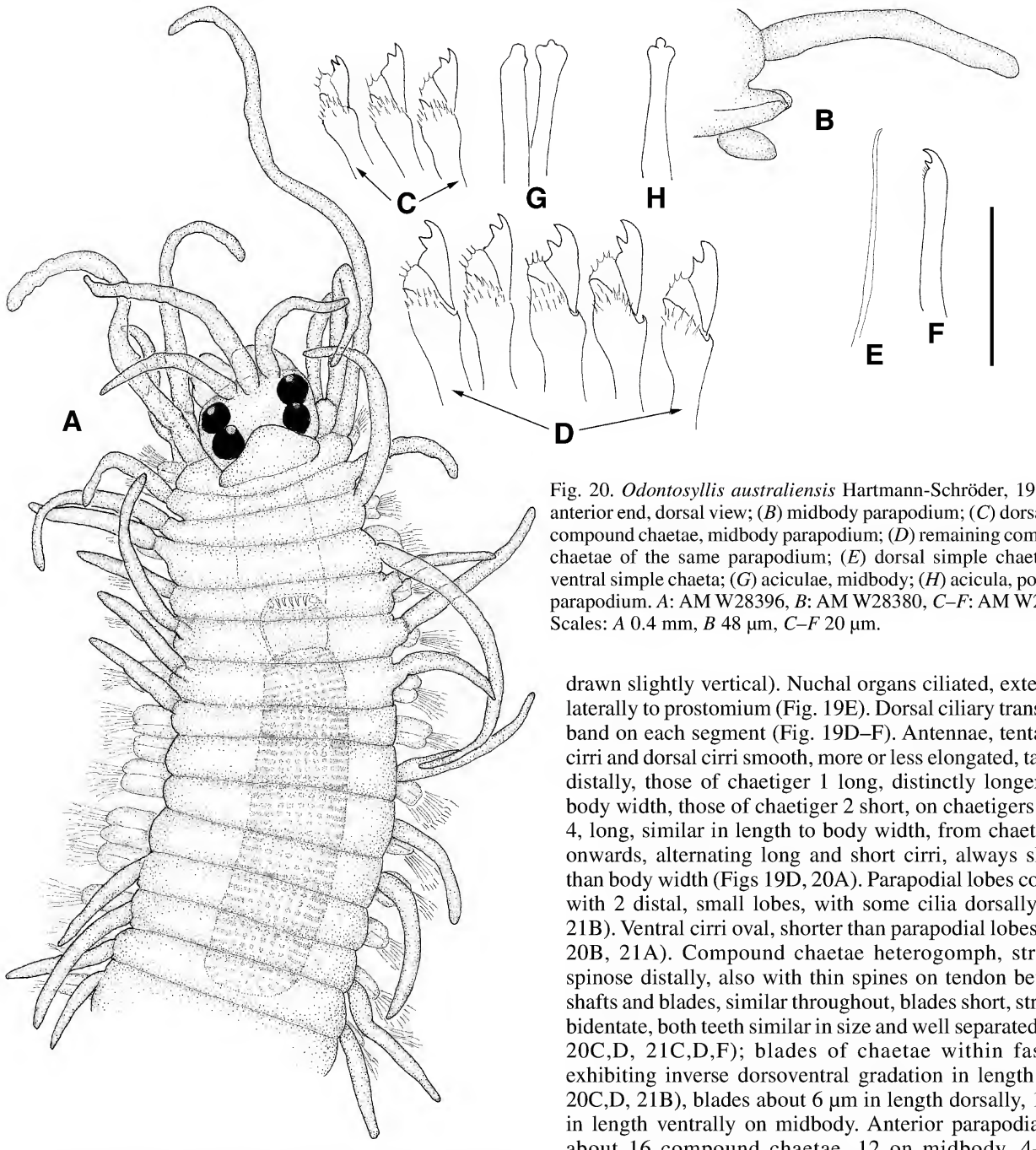


Fig. 20. *Odontosyllis australiensis* Hartmann-Schröder, 1979 (*A*) anterior end, dorsal view; (*B*) midbody parapodium; (*C*) dorsalmost compound chaetae, midbody parapodium; (*D*) remaining compound chaetae of the same parapodium; (*E*) dorsal simple chaeta; (*F*) ventral simple chaeta; (*G*) aciculae, midbody; (*H*) acicula, posterior parapodium. *A*: AM W28396, *B*: AM W28380, *C–F*: AM W28395. Scales: *A* 0.4 mm, *B* 48 µm, *C–F* 20 µm.

Description. Body about 4.4 mm long, 0.3 mm wide, with 44 chaetigers (Fig. 19C); maximum size reported 6.6 mm long for 55 chaetigers (Hartmann-Schröder, 1981), without colour pattern, yellowish in alcohol. Prostomium almost round; 4 eyes in open trapezoidal arrangement, large on epigamic specimens (Fig. 20A). Antennae originating near anterior margin, close to each other, median antenna inserted slightly posterior to lateral ones (Figs 19D,E, 20A), distinctly longer than combined length of prostomium and palps, lateral antennae shorter than median one. Palps shorter than prostomium, ventrally folded (Fig. 21A). Peristomium reduced dorsally, covered by occipital flap (Fig. 19D); dorsal tentacular cirri elongated, nearly twice as long as median antenna, ventral tentacular cirri shorter than dorsal ones. Occipital flap distinct, small, covering posterior margin of prostomium (Figs 19D,E, 20A, Fig. 20A drawn slightly vertical). Nuchal organs ciliated, extending laterally to prostomium (Fig. 19E). Dorsal ciliary transverse band on each segment (Fig. 19D–F). Antennae, tentacular cirri and dorsal cirri smooth, more or less elongated, tapered distally, those of chaetiger 1 long, distinctly longer than body width, those of chaetiger 2 short, on chaetigers 3 and 4, long, similar in length to body width, from chaetiger 5 onwards, alternating long and short cirri, always shorter than body width (Figs 19D, 20A). Parapodial lobes conical, with 2 distal, small lobes, with some cilia dorsally (Fig. 21B). Ventral cirri oval, shorter than parapodial lobes (Figs 20B, 21A). Compound chaetae heterogomph, strongly spinose distally, also with thin spines on tendon between shafts and blades, similar throughout, blades short, strongly bidentate, both teeth similar in size and well separated (Figs 20C,D, 21C,D,F); blades of chaetae within fascicle exhibiting inverse dorsoventral gradation in length (Figs 20C,D, 21B), blades about 6 µm in length dorsally, 12 µm in length ventrally on midbody. Anterior parapodia with about 16 compound chaetae, 12 on midbody, 4–5 on posterior parapodia. Dorsal simple chaetae on posterior parapodia, thin, unidentate (Fig. 20E) (minutely bifid, according to Hartmann-Schröder, 1979), with short spines on margin (Fig. 21E). Ventral simple chaetae on far posterior chaetigers, bidentate, with short spines on margin (Figs 20F, 21F). Aciculae distally knobbed, ending with short terminal process; 3–4 aciculae on anterior parapodia, and 1 on posterior parapodia (Fig. 20G,H). Pharynx short, through 1–2 segments, with 5 teeth and 2 lateral plates. Proventricle long and slender (Fig. 20A), through about 8 segments, with 50 muscle cell rows. Pygidium with 2 anal cirri similar to dorsal ones.

Remarks. This species seems to be similar to *Odontosyllis hyalina* Grube, 1878 from Singapore; the description of that species was made on the basis of a single, epigamic specimen, in which some characters can be modified in

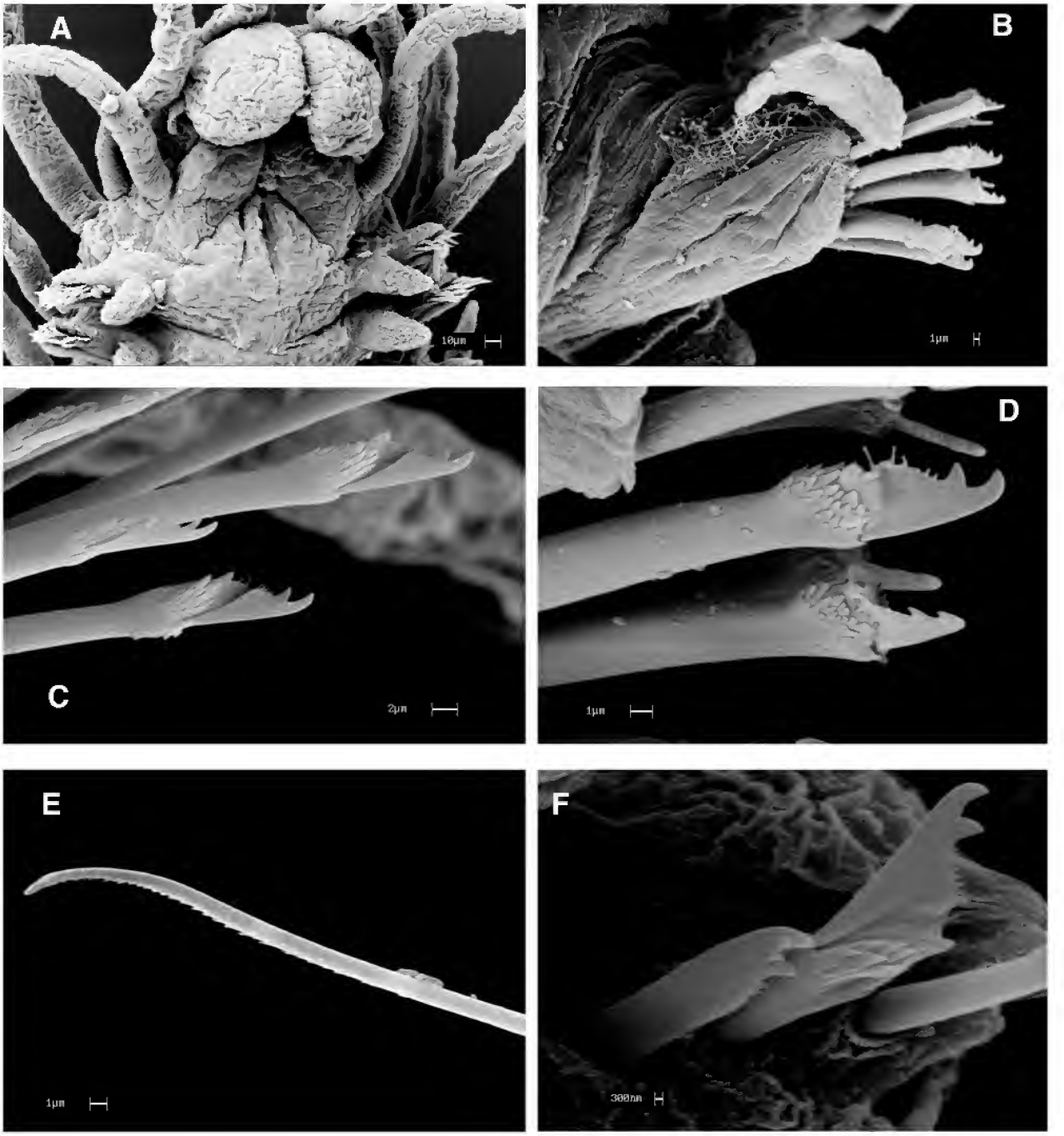


Fig. 21. SEM of *Odontosyllis australiensis* Hartmann-Schröder, 1979 (*A*) prostomium and anteriormost segments, ventral view; (*B*) posterior parapodium; (*C,D*): compound chaetae, midbody; (*E*) dorsal simple chaeta; (*F*) ventral simple and compound chaetae. AM W28380.

comparison to non-epigamic specimens, and it is difficult to assess if both species are valid or synonymous. The syntype (MPUW, 325) is in poor condition, covered by crystals of formalin, but the chaetae appear different (see above); so at this stage we are accepting both species as valid.

Habitat. Occurring on algae, dead coral and coarse sediments, from intertidal to shallow depths.

Distribution. Australia (Western Australia, New South Wales, Queensland).

Odontosyllis detecta Augener, 1913

Fig. 22A–C

Odontosyllis detecta Augener, 1913: 236, pl. III, Fig. 33, text-fig. 34; 1927: 153.—Haswell, 1920: 105.—Imajima, 1966: 103, figs 33a–m.—Hartmann-Schröder, 1985: 69.—San Martín, 1990: 613, fig. 16.

Material examined. AUSTRALIA: NEW SOUTH WALES: Port Jackson, 33°51'S 151°16'E, donated by W.A. Haswell, Feb 1920, 1 (slide) (AM W501).

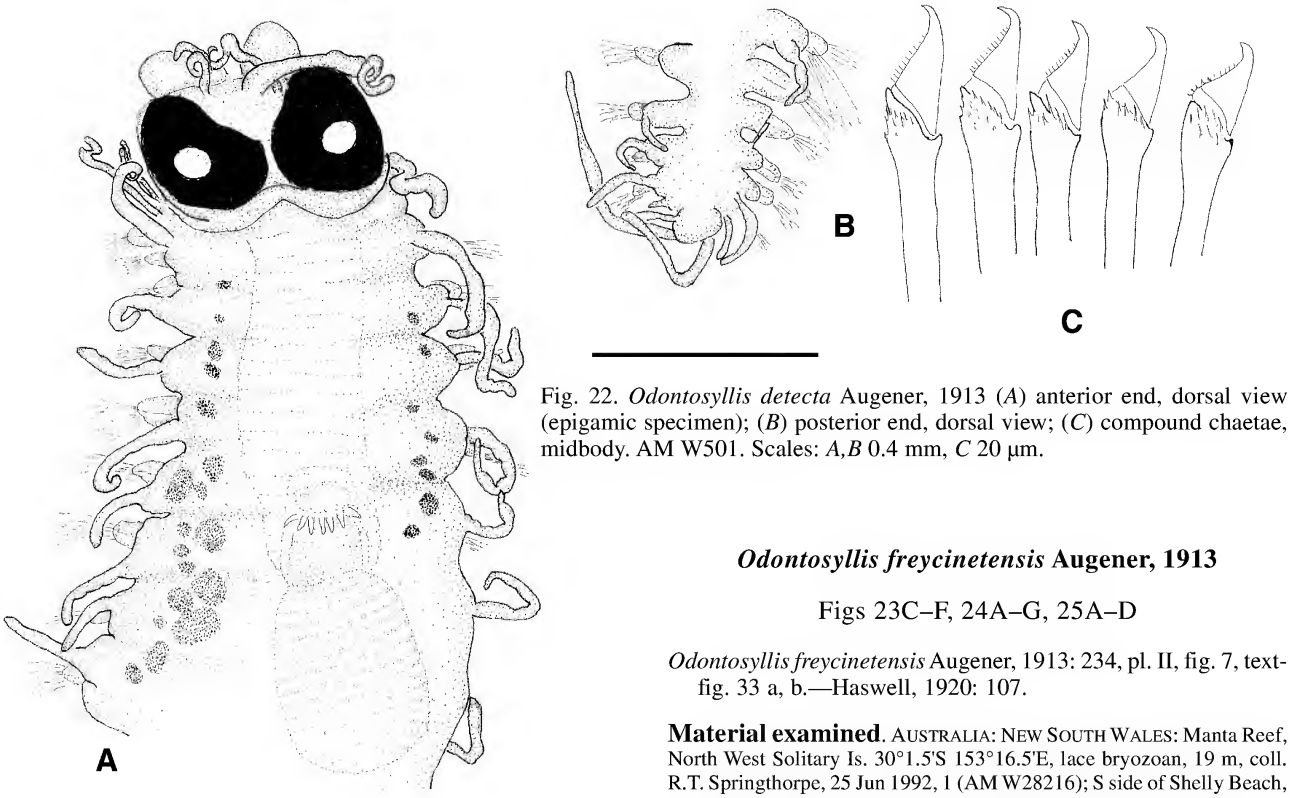


Fig. 22. *Odontosyllis detecta* Augener, 1913 (*A*) anterior end, dorsal view (epigamic specimen); (*B*) posterior end, dorsal view; (*C*) compound chaetae, midbody. AM W501. Scales: *A,B* 0.4 mm, *C* 20 μm.

Description. Only examined specimen, mature, epigamic male, 5 mm long, 0.1 mm wide, with 37 chaetigers, on permanent, stained slide. Adult, non-epigamic specimens from Japan, 6–9 mm long, 1 mm wide, with 40–52 chaetigers (Imajima, 1966). Specimen from Port Jackson with 2 large, black eyes, small palps and coiled cirri (Fig. 22A). Occipital flap absent. 4–5 compound chaetae per parapodium, with distally spinose shafts and short, curved, unidentate blades, with short spines on margin (Fig. 22C). Dorsal simple chaetae from midbody, thin, unidentate, smooth. Ventral simple chaetae absent. Acicula solitary, distally knobbed, with short tip. Pharynx through 2 segments, with 5 teeth and 2 lateral plates. Proventricle through 2 segments (Fig. 22A). Pygidium semi-circular, with 2 long anal cirri, extending for 6 chaetigers (Fig. 22B).

Japanese non epigamic specimens (fide Imajima, 1966), with antennae, dorsum and dorsal cirri dark red; with ciliary bands across dorsum, nuchal ridges present; lacking occipital flap. Dorsal cirri alternating in length, shorter than body width, and ventral simple chaetae on posterior parapodia, unidentate, slightly hooked, with short, fine spines on margin.

Remarks. As the only Australian material available for examination was a mature epigamic male, it is difficult to relate this to the non epigamic individuals recorded from Japan by Imajima (1966), but we believe them to represent the same species.

Habitat. Occurring in sand, seagrass, algae; intertidally.

Distribution. Australia (Western Australia, South Australia, New South Wales), Japan, Cuba.

Odontosyllis freycinetensis Augener, 1913

Figs 23C–F, 24A–G, 25A–D

Odontosyllis freycinetensis Augener, 1913: 234, pl. II, fig. 7, text-fig. 33 a, b.—Haswell, 1920: 107.

Material examined. AUSTRALIA: NEW SOUTH WALES: Manta Reef, North West Solitary Is. 30°1.5'S 153°16.5'E, lace bryozoan, 19 m, coll. R.T. Springthorpe, 25 Jun 1992, 1 (AM W28216); S side of Shelly Beach, Fairy Bower, 33°48.18'S 151°17.4'E, in between large boulders & under small ones, 8 m, coll. P.A Hutchings, 24 Oct 1971, 1 on SEM stub (AM W24679); Grotto Point, Port Jackson, 33°49'S 151°15'E, algae, 4 m, coll. P. Colman, 18 July 1983, 1 (AM W28915); Summer Cloud Bay, Wreck Bay, 35°10.5'S 150°41'E, 15 m, coll. P.A. Hutchings, 29 Nov 1971, 1 (AM W26325). WESTERN AUSTRALIA: Off S end of Long Is. Beacon Is. 28°28.8'S 113°46.3'E, dead coral substrate covered in coralline algae, 4.5 m, coll. P.A. Hutchings, 25 May 1994, 2 (AM W28390).

Description. Body broad anteriorly, tapered posteriorly (Fig. 23C), largest complete specimen examined 10 mm long, 0.5 mm wide, with 59 chaetigers, sometimes without colour pattern, but usually with 2–3 dark, dorsal spots on some anterior chaetigers (Fig. 24A), others dark. Prostomium oval, large, with long cilia laterally (Fig. 24A); 4 eyes in open trapezoidal arrangement; antennae short, fusiform, shorter than prostomium (Figs 23D, 24A), median antenna originating between anterior eyes, lateral antennae near anterior margin of prostomium, close to median antennae. Palps small, shorter than prostomium, ventrally folded (Fig. 24A). Nuchal organs distinct, with long cilia between prostomium and peristomium (Figs 23D, 24A). Peristomium distinct, similar in length to subsequent segments. Occipital flap covering posterior part of prostomium (Figs 23D, 24A). Tentacular cirri similar in shape to antennae, but longer. Dorsal cirri fusiform, some more elongated than antennae, those of chaetiger 1 slightly longer than others, shorter than half of body width, slightly longer than parapodial lobes (Figs 23E, 24C). Parapodial lobes elongated, almost rectangular, distally bilobed (Figs 23E, 24C); anterior parapodia with distal, digitiform papilla; progressively, posteriorly parapodia becoming more elongated, and distinctly bilobed distally, and distal papilla becoming fused. Ventral cirri digitiform, elongated, reaching or extending beyond parapodial lobes (Fig. 24C). Compound chaetae slender, with elongated, unidentate blades, with slightly hooked tips (Figs 23F, 24E,F, 25A),

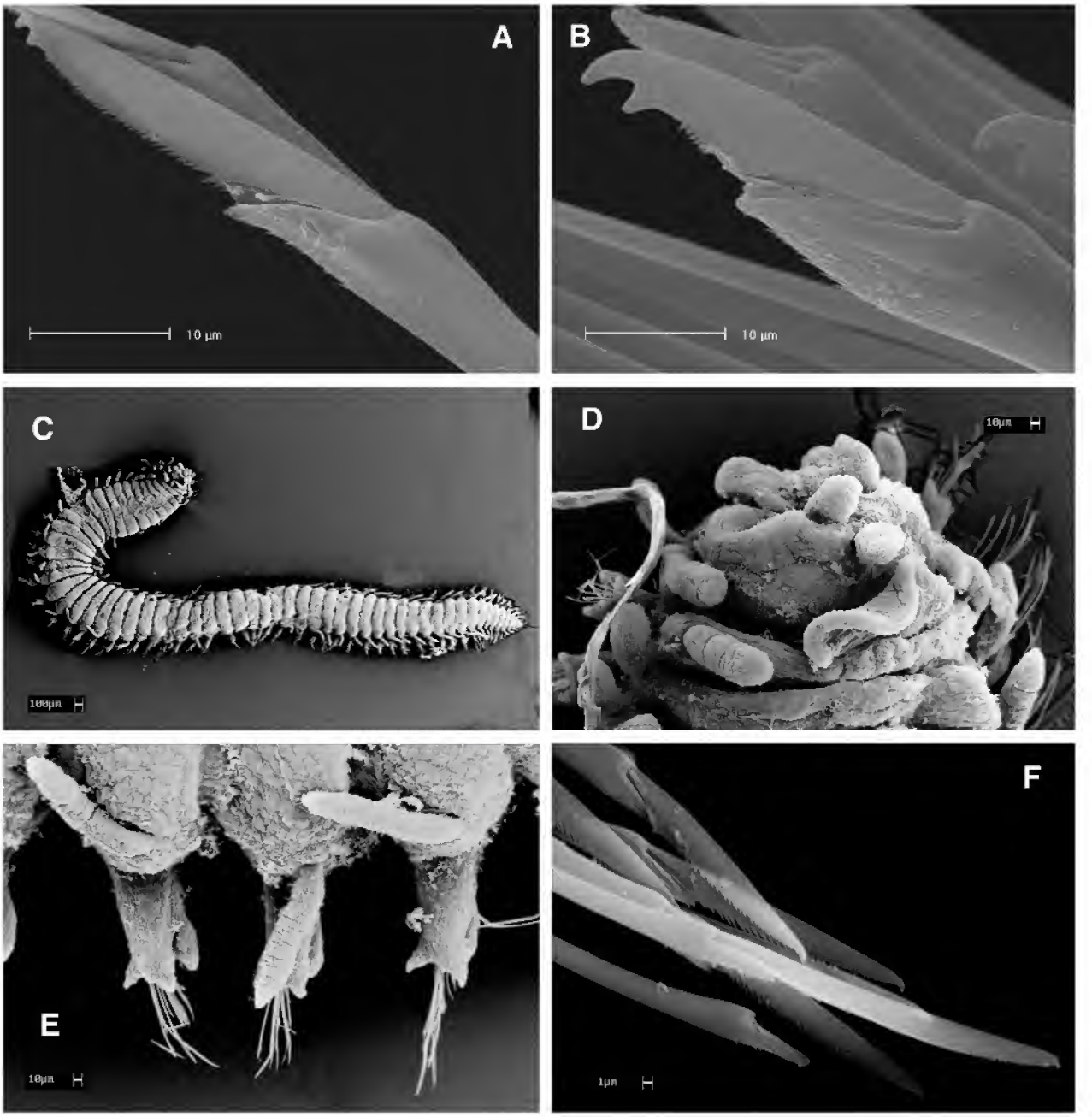


Fig. 23. SEM of *Odontosyllis marombibooral* n.sp. (*A*) dorsal compound chaeta, posterior parapodium; (*B*) ventral compound chaeta, posterior parapodium. SEM of *Odontosyllis freycinetensis* Augener, 1913 (*C*) complete specimen, dorsal view; (*D*) prostomium and anteriormost segments; (*E*) midbody parapodia, dorsal view; (*F*) anterior compound chaetae. *A,B*: AM W5496, *C–F*: AM W24679.

with margins either smooth or with short spines. Anterior parapodia with about 16–18 compound chaetae, with dorsoventral gradation in length of blades within fascicle, 40 µm in length dorsally, 20 µm in length ventrally; number of compound chaetae per parapodium decreasing posteriorly, up to about 9 on posterior parapodia, blades of similar lengths to anterior ones; blades with short, minute subdistal spine (Fig. 25B–D, arrows). Dorsal and ventral simple chaetae on posterior parapodia, thin, smooth, dorsal ones bifid (Fig. 24H) and ventral unidentate (Fig. 24I). Anterior parapodia with 2–3 aciculae, becoming solitary after proventricular segments, distally acuminate (Fig. 24D,G). Pharynx wide, through 2–3 segments, with 5 teeth and 2 lateral plates. Proventricle wide, short, slightly longer than pharynx (Fig. 24A), through about 4 segments, with 28–30 muscle cell rows. Pygidium rectangular, small, with 2 lateral, short anal cirri, and 1 median, digitiform papilla (Fig. 24B).

Habitat. Occurring on algae, bryozoans, dead corals; intertidal and shallow depths.

Distribution. Australia (Western Australia, New South Wales).

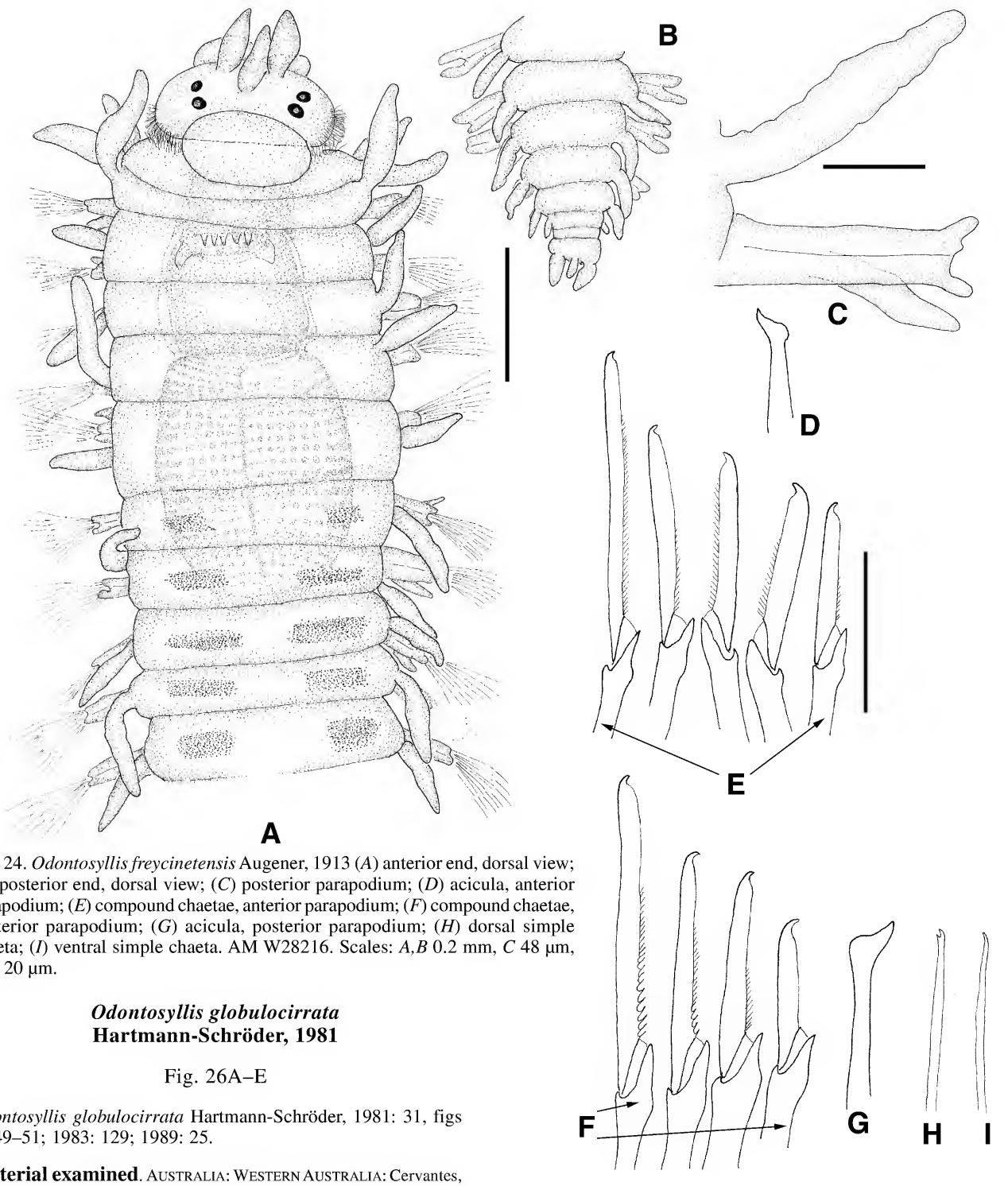


Fig. 24. *Odontosyllis freycinetensis* Augener, 1913 (*A*) anterior end, dorsal view; (*B*) posterior end, dorsal view; (*C*) posterior parapodium; (*D*) acicula, anterior parapodium; (*E*) compound chaetae, anterior parapodium; (*F*) compound chaetae, posterior parapodium; (*G*) acicula, posterior parapodium; (*H*) dorsal simple chaeta; (*I*) ventral simple chaeta. AM W28216. Scales: *A,B* 0.2 mm, *C* 48 µm, *D–I* 20 µm.

Odontosyllis globulocirrata Hartmann-Schröder, 1981

Fig. 26A–E

Odontosyllis globulocirrata Hartmann-Schröder, 1981: 31, figs 49–51; 1983: 129; 1989: 25.

Material examined. AUSTRALIA: WESTERN AUSTRALIA: Cervantes, 30°30'S 115°03'E, fine sand with *Posidonia*, coll. G. Hartmann-Schröder, 24 Oct 1972, 2 paratypes (AM W17725). NEW SOUTH WALES: Halfway Reef, 200 m S of Sullivan Reef, Ulladulla, 35°21'25"S 150°29'19"E, airlift over wall of sponges, Bryozoa, Hydrozoa, 15m, coll. P.B. Berents, K.B. Attwood & A. Murray, 3 May 1997, 1 (AM W29375).

Description. Paratype examined 8.1 mm long, 0.8 mm wide, with 43 chaetigers; holotype 10 mm long for 48 chaetigers according to Hartmann-Schröder. Body broad anteriorly, tapering posteriorly, lightly coloured on dorsum of some segments, with 2–4 dark spots (Fig. 26A). Prostomium oval, about 3 times wider than long; 4 eyes arranged in open trapezoidal pattern, posterior ones covered by occipital flap (Fig. 26A); antennae short, globular, median antenna slightly longer than lateral ones (Fig. 26A,B), originating between anterior eyes, lateral antennae inserted on anterior margin of prostomium. Palps small, short. Peristomium dorsally reduced (Fig. 26A,B). Tentacular cirri globular, similar in size to antennae. Occipital flap oval, covering only posterior margin of prostomium (Fig. 26A,B). Dorsal cirri globular, sphaerical, shorter than parapodial lobes, those inserted dorsolaterally on chaetigers 1, 4, and 6-8-10-..., slightly larger and more elongate than those on chaetigers 2, 3, 5-7-

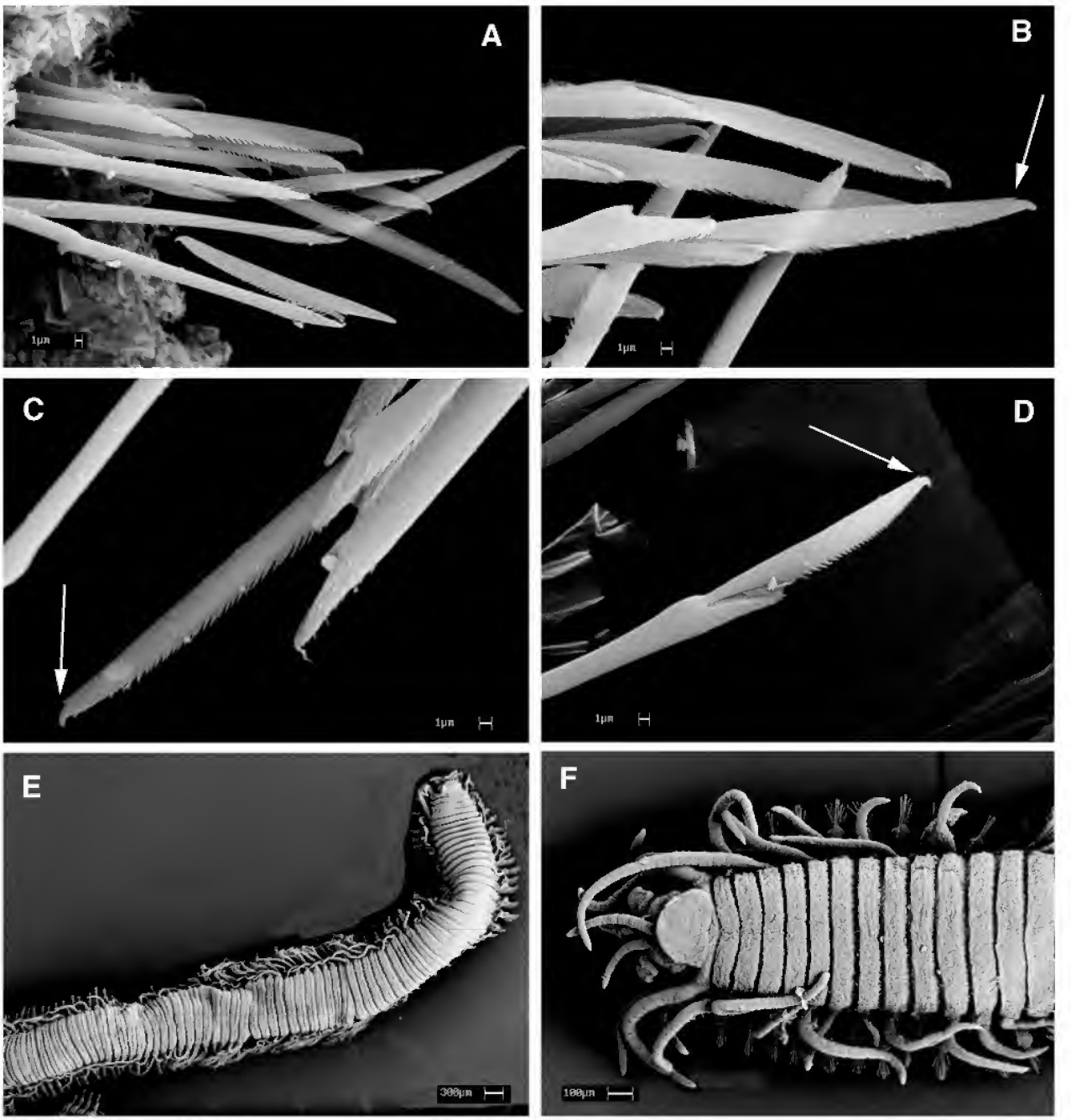


Fig. 25. SEM of *Odontosyllis freycinetensis* Augener, 1913 (*A,B*), compound chaetae, midbody; (*C*) long-bladed compound chaeta, midbody; (*D*) short bladed compound chaeta, midbody. SEM of *Odontosyllis polycera* Schmarda, 1863 (*E*) anterior end and midbody, dorsal view; (*F*) anterior end, dorsal view. *A–D*: AM W24679, *E*: AM W195387, *F*: AM W194258.

9-…, inserted adjacent to parapodial lobes (Fig. 26B,C). Parapodial lobes elongated, distinctly bilobed distally (Fig. 26A–C). Ventral cirri short, conical, inserted near distal part of parapodial lobes. Compound chaetae numerous, about 20 on midbody parapodia, with smooth shafts, or provided with minute subdistal spines, and elongate, unidentate blades, distally slightly hooked, provided with short, fine spines on margin (Fig. 26E), blades of chaetae within fascicle exhibiting dorsoventral gradation in length, about 33 µm in length dorsally, 25 µm in length ventrally. Dorsal and ventral simple chaetae not seen nor previously described. Aciculae solitary, slender, straight. Pharynx wide, short, with 7 teeth (fide Hartmann-Schröder; not seen in material examined) and 2 lateral plates. Proventricle large, 2.5× longer than pharynx (Fig. 26D), with about 40 muscle cell rows. Pygidium with 2 globular anal cirri, similar to dorsal ones.

Habitat. Occurring on algae and sediment, intertidal.

Distribution. Australia (Western Australia, New South Wales).

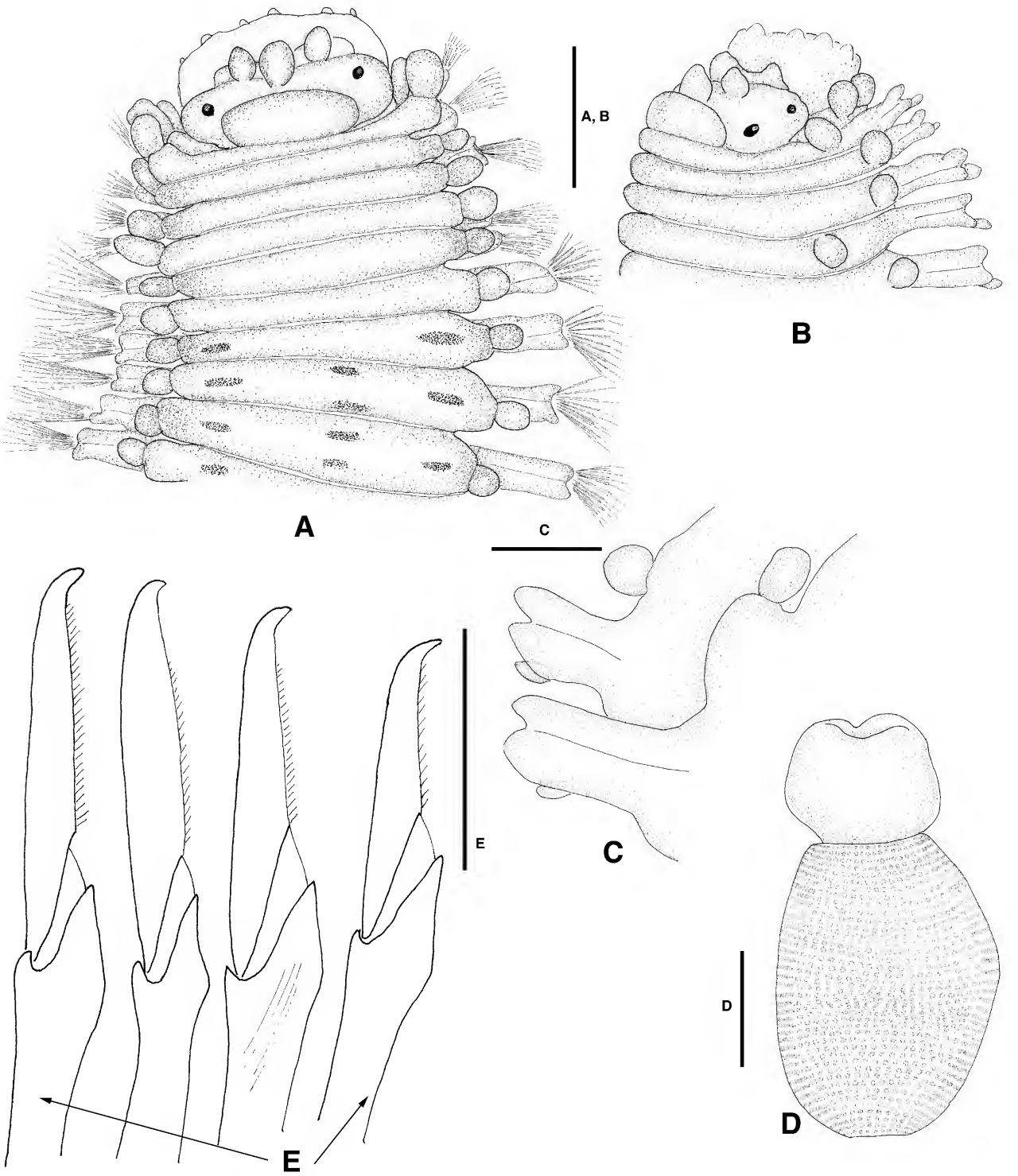


Fig. 26. *Odontosyllis globulocirrata* Hartmann-Schröder, 1981 (*A*) anterior end, dorsal view; (*B*) anterior end, dorsolateral view; (*C*) midbody parapodia; (*D*) pharynx and proventricle; (*E*) compound chaetae, midbody. AM W17725. Scales: *A,B* 0.4 mm, *C* 0.1 mm, *D* 0.4 mm, *E* 20 µm.

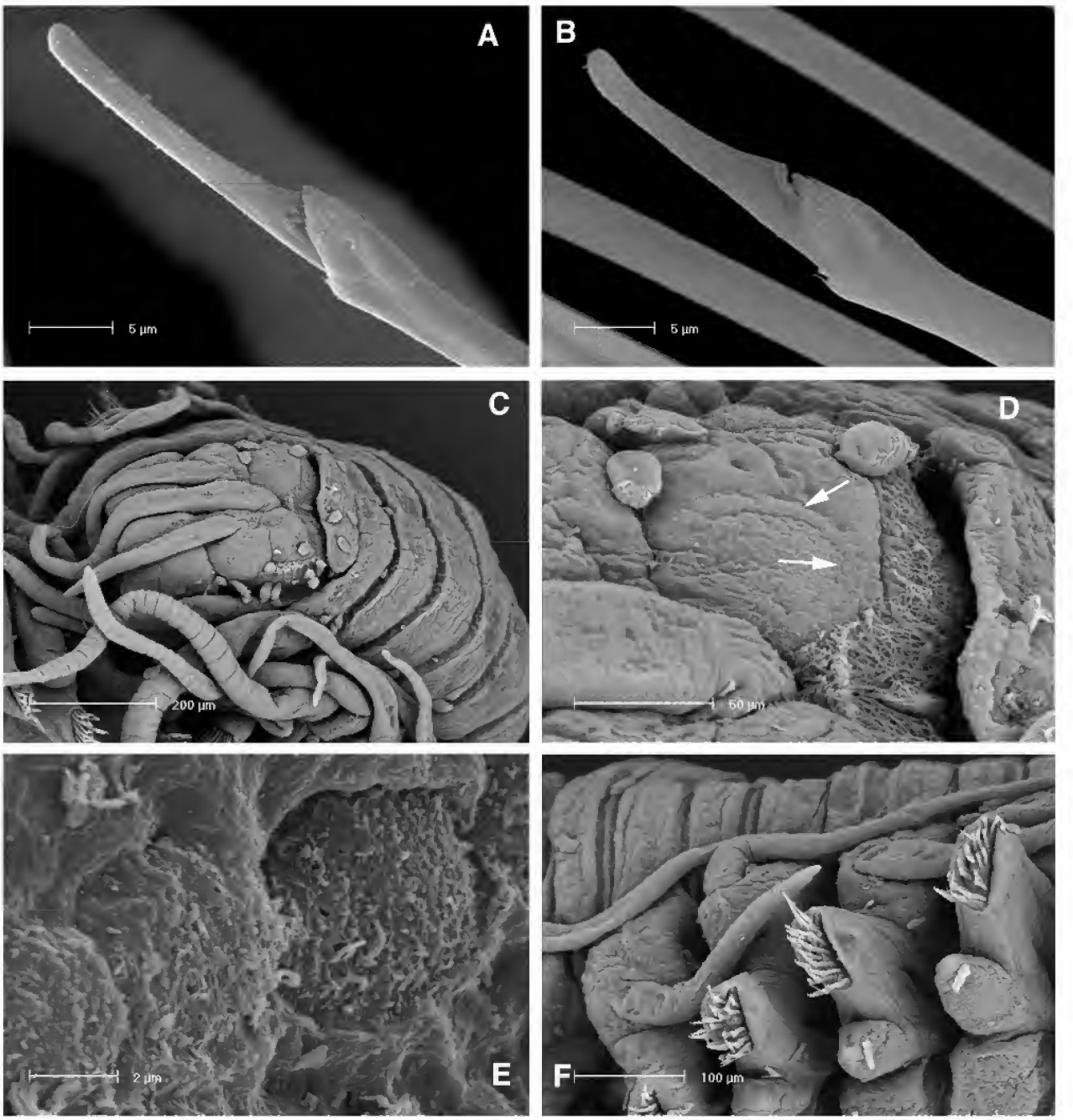


Fig. 27. SEM of *Odontosyllis langerhansiaesetosa* Hartmann-Schröder, 1979 (*A*) long falciger, midbody; (*B*) short falciger, midbody. SEM of *Odontosyllis gravelyi* n.sp. (*C*) anterior end, dorsal view; (*D*) detail of prostomium (arrows showing the mounds with minute pores); (*E*) detail of mounds with pores on prostomium; (*F*) midbody parapodia. *A,B*: AM W198069, W202639; *C–F*: AM W202645.

Odontosyllis gravelyi Fauvel, 1930

Figs 27C–F, 28A–H, 29A–F

Odontosyllis gravelyi Fauvel, 1930: 16, figs. 3–4; 1953: 160, figs. 81–82.

Material examined. AUSTRALIA: NEW SOUTH WALES: Careel Bay, Pittwater, 33°37'S 151°19'E, *Zostera*, coll. P.A. Hutchings, 4 Nov 1973 (AM W11110). QUEENSLAND: Calliope R., 23°51'S 151°10'E, coll. P. Saenger, 1974, 7 (AM W199367). Triangular Islets, Shoalwater Bay, 22°23'S 150°31'E, coll. J.A. Lewis & J.R. Forsyth, 1981, 10 on SEM stub (AM W202645).

Description. Body 14 mm long, 1.2 mm wide, with 50 chaetigers; distinct, median longitudinal black band, and large lateral spots, resembling 3 longitudinal stripes (Fig. 28A). Prostomium small, hidden under most anterior segments (Figs 27C, 28A–C) (probably contracted), with 2 black lateral spots and posterior transverse band; antennae short and slender, inserted in front of anterior eyes, median antenna longer than lateral antennae, inserted slightly posteriorly (Figs 27C, 28B,C), similar to combined length of prostomium and palps. Prostomium with 2 slightly raised mounds with minute pores (see arrows Fig. 27D,E). Two densely ciliated, semi-circular nuchal organs (Fig. 27C,D). Palps small, fused basally, ventrally folded. Peristomium

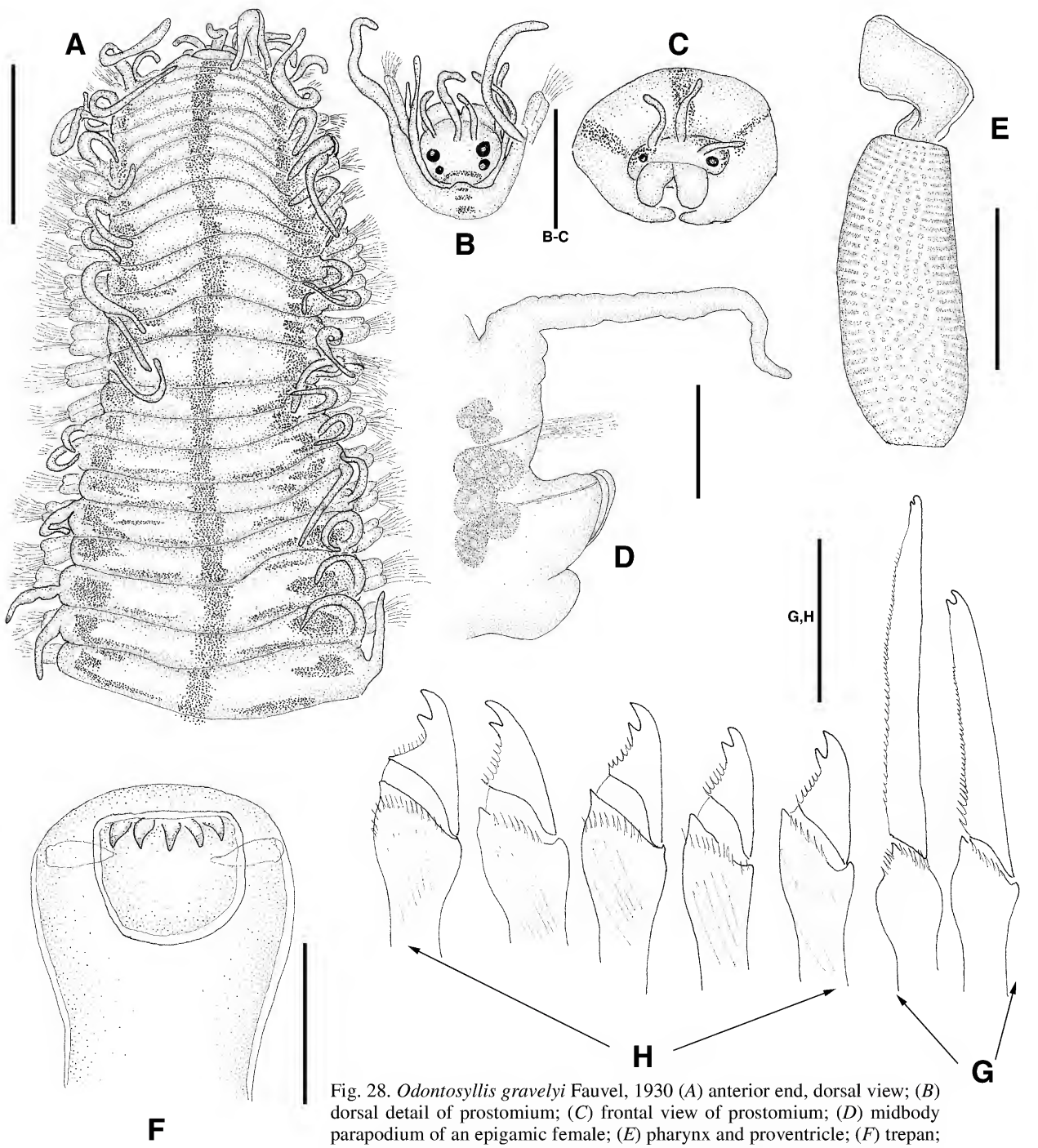


Fig. 28. *Odontosyllis gravelyi* Fauvel, 1930 (*A*) anterior end, dorsal view; (*B*) dorsal detail of prostomium; (*C*) frontal view of prostomium; (*D*) midbody parapodium of an epigamic female; (*E*) pharynx and proventricle; (*F*) trepan; (*G*) long-bladed compound chaetae, midbody; (*H*) falcigers, midbody. Holotype AM W11110, except *B*, AM W202645. Scales: *A–C,E*: 0.8 mm, *D*: 0.2 mm, *F*: 0.18 mm, *G,H*: 20 µm.

small, dorsally nearly covered by small lobe of chaetiger 1 (Figs 27C, 28B); tentacular cirri similar to antennae, but slightly longer. Anterior dorsal cirri elongated, smooth, distally tapered, rugose to pseudoarticulate (Figs 27C, 28A) becoming progressively shorter along body (Figs 27F, 28D), slightly longer than parapodial lobes. Parapodia with 2–3 parallel lobes (Figs 27F, 28D, 29A). Ventral cirri short, pillow-shaped (Figs 27F, 28D). Compound chaetae numerous, shafts distally spinose, and blades of 2 kinds, most dorsal ones with elongate, bidentate blades (Fig. 28G), short spines on margin, and remaining chaetae with short, triangular, distinctly bidentate blades (Figs 28H, 29A–E); on midbody, parapodia with about 6–7 compound chaetae of slender type, 37–45 µm in length, and 28–30 chaetae with short blades, all similar, about 16–18 µm in length; compound chaetae slightly longer on anterior parapodia (Fig. 29A,B). Aciculae slender, distally blunt, numerous in anterior parapodia, reduced to 2–3 on posterior parapodia. Dorsal simple chaetae slender, thin, unidentate (Fig. 29C). Ventral simple chaetae on posterior parapodia, bidentate, with short spines on margin (Fig. 29C,F). Pharynx through 3–4 segments, with 5 teeth and 2 lateral plates (Fig. 28F). Proventricle long, slender (Fig. 28E), through 9 segments, with about 80 muscle cell rows.

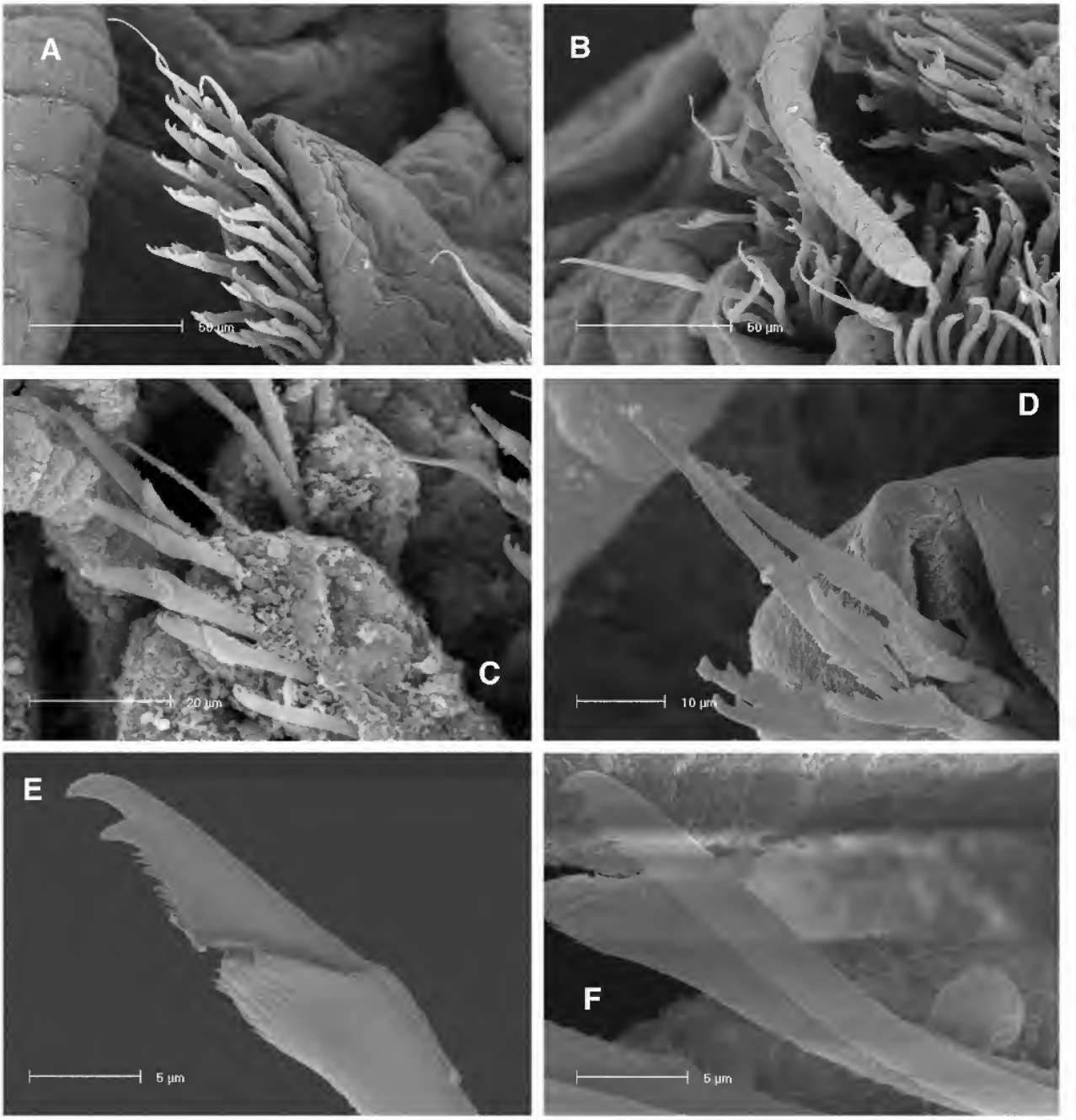


Fig. 29. SEM of *Odontosyllis gravelyi* Fauvel, 1930 (*A*) chaetal fascicle, anterior parapodium; (*B*) chaetal fascicles, midbody parapodia; (*C*) chaetal fascicle, posterior parapodium; (*D*) compound chaetae, posterior parapodium; (*E*) falciger, midbody; (*F*) ventral simple chaeta. AM W11110.

Remarks. The small lobe on the peristomium is not regarded as an occipital flap. This species is characterized by its colour pattern, a lack of an occipital flap, and two kinds of compound chaetae being present. *Odontosyllis trilineata* Imajima, 2003 has a similar colour pattern and chaetae, but they differ in that *O. gravelyi* also has long-bladed chaetae, and *O. trilineata* has a distinct occipital flap and 9 teeth on trepan (Imajima, 2003).

Habitat. Occurring in coarse sand and gravel and mud, shallow depths often in estuarine conditions.

Distribution. Australia (New South Wales, Queensland) and southeast India.

Odontosyllis langerhansiaesetosa Hartmann-Schröder, 1979

Figs 27A,B, 30A–K, 31A–F

Odontosyllis langerhansiaesetosa Hartmann-Schröder, 1979: 94, figs 91–96; 1980: 50; 1990: 51.

Material examined. AUSTRALIA: QUEENSLAND: Triangular Islets, Shoalwater Bay, 22°23'S 150°31'E, coll. J.A. Lewis & J.R. Forsyth, 1981, 5 + 1 on SEM stub (AM W202639); Calliope R., 23°51'S 151°10'E, coll. P. Saenger, 1974, few (AM W28947); Auckland Creek, Gladstone, 23°51'S 151°14'E, coarse gravel, 1.3 m, coll. P. Saenger, Apr 1977, 1 (AM W198068); Auckland Creek, Gladstone, 23°51'S 151°14'E, coarse sand, 2.8 m, coll. P. Saenger, July 1979, 1 on SEM stub (AM W198069); Branch of Calliope R., Gladstone, 23°51'S 151°10'E, coarse gravel, 2.3

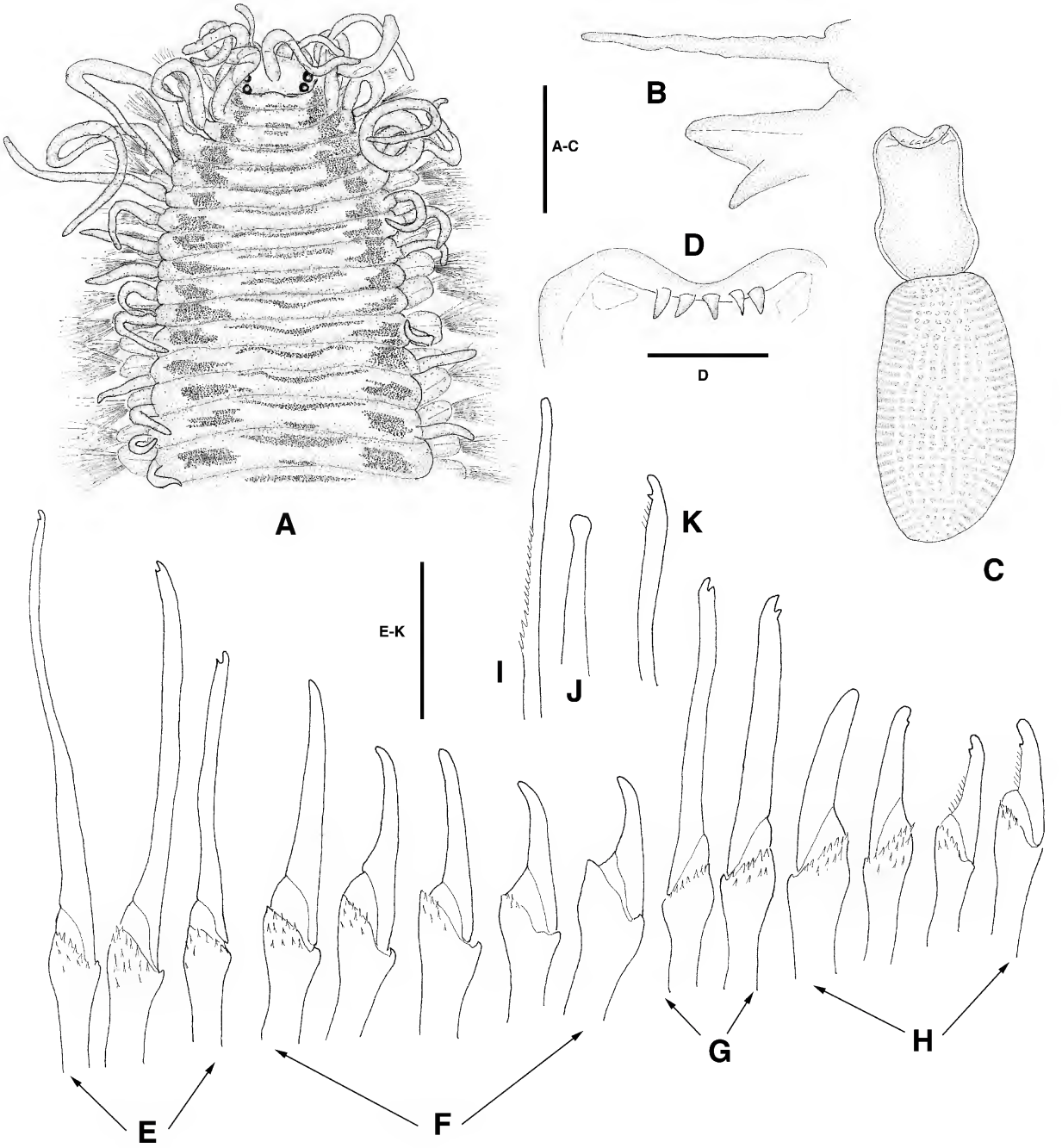


Fig. 30. *Odontosyllis langerhansiaesetosa* Hartmann-Schröder, 1979 (*A*) anterior end, dorsal view; (*B*) midbody parapodium; (*C*) pharynx and proventricle; (*D*) trepan; (*E*) long-bladed compound chaetae, anterior parapodium; (*F*) falcigers, anterior parapodium; (*G*) long-bladed compound chaetae, posterior parapodium; (*H*) falcigers, posterior parapodium; (*I*) dorsal simple chaeta; (*J*) acicula; (*K*) ventral simple chaeta. *A,B,E–K*: AM W198073; *C*: AM W198068. Scales: *A* 0.4 mm, *B* 0.18 mm, *C* 0.1 mm, *D* 0.2 mm, *E–K* 20 μm.

m, P. Saenger, July 1979, 1 (AM W198070); Calliope R., Gladstone, 23°51'S 151°10'E, silty sand, 3.4 m, P. Saenger, July 1979, 1 (AM W198071); Auckland Creek, Gladstone, 23°51'S 151°14'E, coarse sand, 2.3 m, coll. P. Saenger, July 1979, 1 (AM W198072); Black Harry Creek, Gladstone, 23°51'S 151°10'E, soft mud, 0.7 m, coll. P. Saenger, Sept. 1981, 1 (AM W198073). NEW SOUTH WALES: Green Point, Hawkesbury R., 33°34'S 151°14'E, mud, 12 m, coll. A. Jones & party, 13 Nov 1979, 1 (AM W28946).

Description. Body broad anteriorly, tapered posteriorly, up to 9.6 mm long, 0.9 mm wide, 72 chaetigers; colour pattern variable, some apparently lacking pigmentation to others, dark, with distinct pattern (Fig. 30A) of dark band on dorsum of each anterior segment, split into 3 or more spots, and sometimes on midbody segments. Prostomium oval, about twice as wide as long; 4 eyes in trapezoidal arrangement. Median antenna longer than combined length of prostomium and palps, originating on middle of prostomium; lateral antennae about half of length of median one, inserted on anterior margin of prostomium (Figs 30A, 31A). Palps short, ventrally folded (Fig. 31C). Peristomium distinct dorsally, slightly shorter than subsequent segments (Figs 30A, 31A), with dorsal, small lobe covering posterior margin of prostomium (Fig. 30A). Occipital flap absent. Tentacular cirri and most anterior dorsal cirri elongated, longer than body width (Figs 30A, 31A), smooth; remaining dorsal cirri shorter (Figs 30A, 31B), slightly longer than parapodial lobes, distally tapered (Figs 30B, 31D). Parapodial lobes

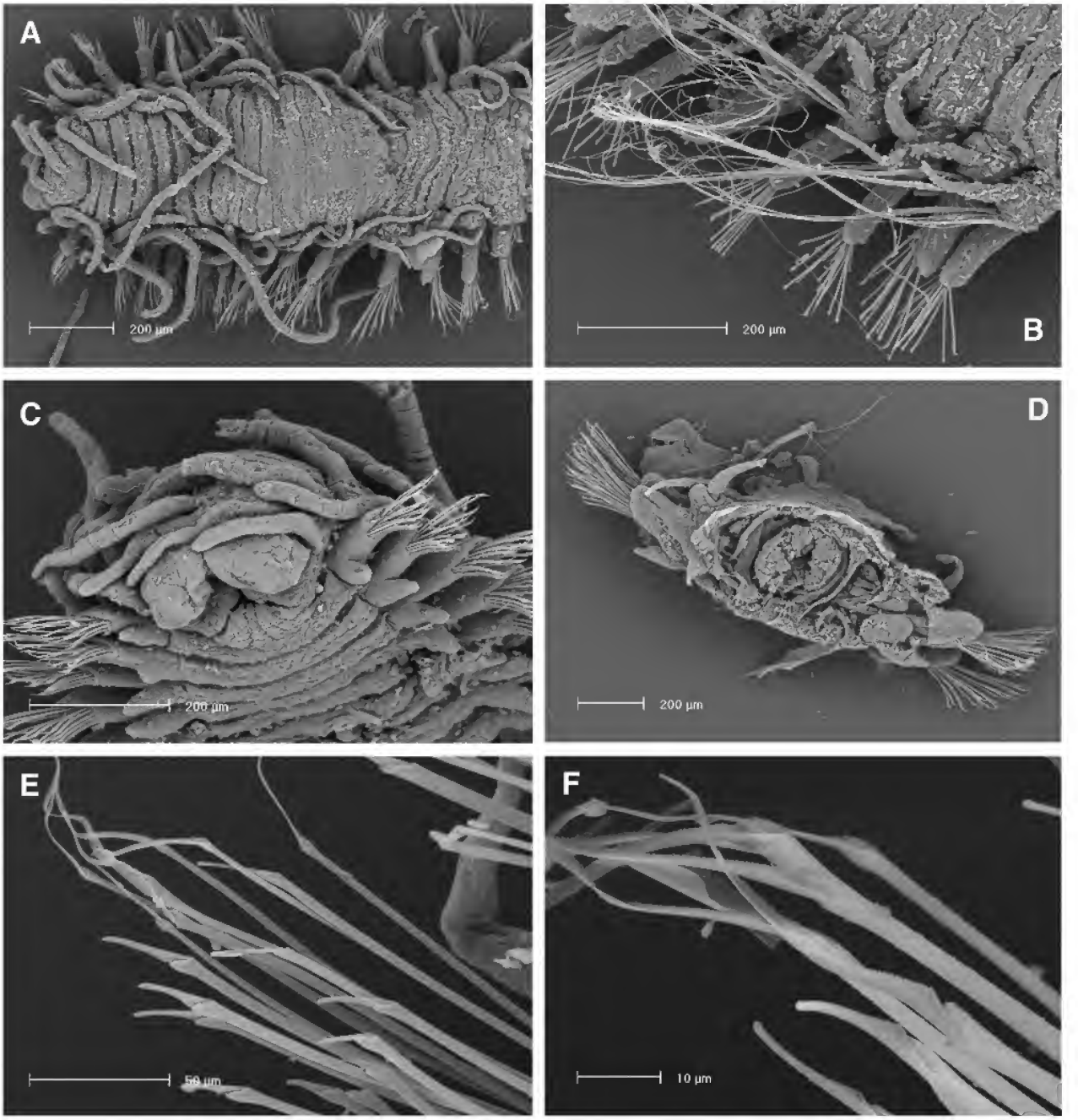


Fig. 31. SEM of *Odontosyllis langerhansiaesetosa* Hartmann-Schröder, 1979 (*A*) anterior end, dorsal view; (*B*) midbody parapodia of an epigamic specimen, showing the natatory chaetae; (*C*) anterior end, ventral view; (*D*) cross section of a midbody segment; (*E,F*) compound chaetae, anterior parapodium. AM W198069, W202639.

conical; ventral cirri triangular to digitiform, shorter than parapodial lobes. Compound chaetae with spinose shafts and 2 kinds of blades; most superior chaetae with elongated, slender, distally bidentate blades (Figs 30E,G, 31E,F), margin smooth, and others similar but blades shorter, unidentate or weakly bidentate (Figs 30F,H, 27A,B); tendon partially fused to blades. Anterior parapodia with about 6 long-bladed chaetae, 38–60 µm long, and 10 short-bladed chaetae, with dorsoventral gradation in length of blades, 35 µm in length dorsally, 18 µm in length ventrally. Progressively along body, number of compound chaetae per parapodium decreasing to 4 long-bladed, 37–40 µm in length, and 4–5 short bladed, 25 µm in length dorsally, 15 µm in length ventrally. Dorsal simple chaetae on posterior parapodia, slender, unidentate, distally blunt, with some short, subdistal spines on margin (Fig. 30I). Ventral simple chaetae on most posterior parapodia, bidentate, with fine spines on margin (Fig. 30K). Several aciculae on anterior parapodia, decreasing to 1 on posterior parapodia, slender, distally knobbed (Fig. 30J). Pharynx about half of length of proventricle (Fig. 30C), through about 6 segments, with 5 teeth and 2 lateral plates (Fig. 30D). Proventricle through about 9–10 segments, with 50 muscle cell rows.

Habitat. Occurring in coarse sand, silt, gravel, mud, from intertidal to shallow depths.

Distribution. Australia (Western Australia, Queensland, New South Wales).

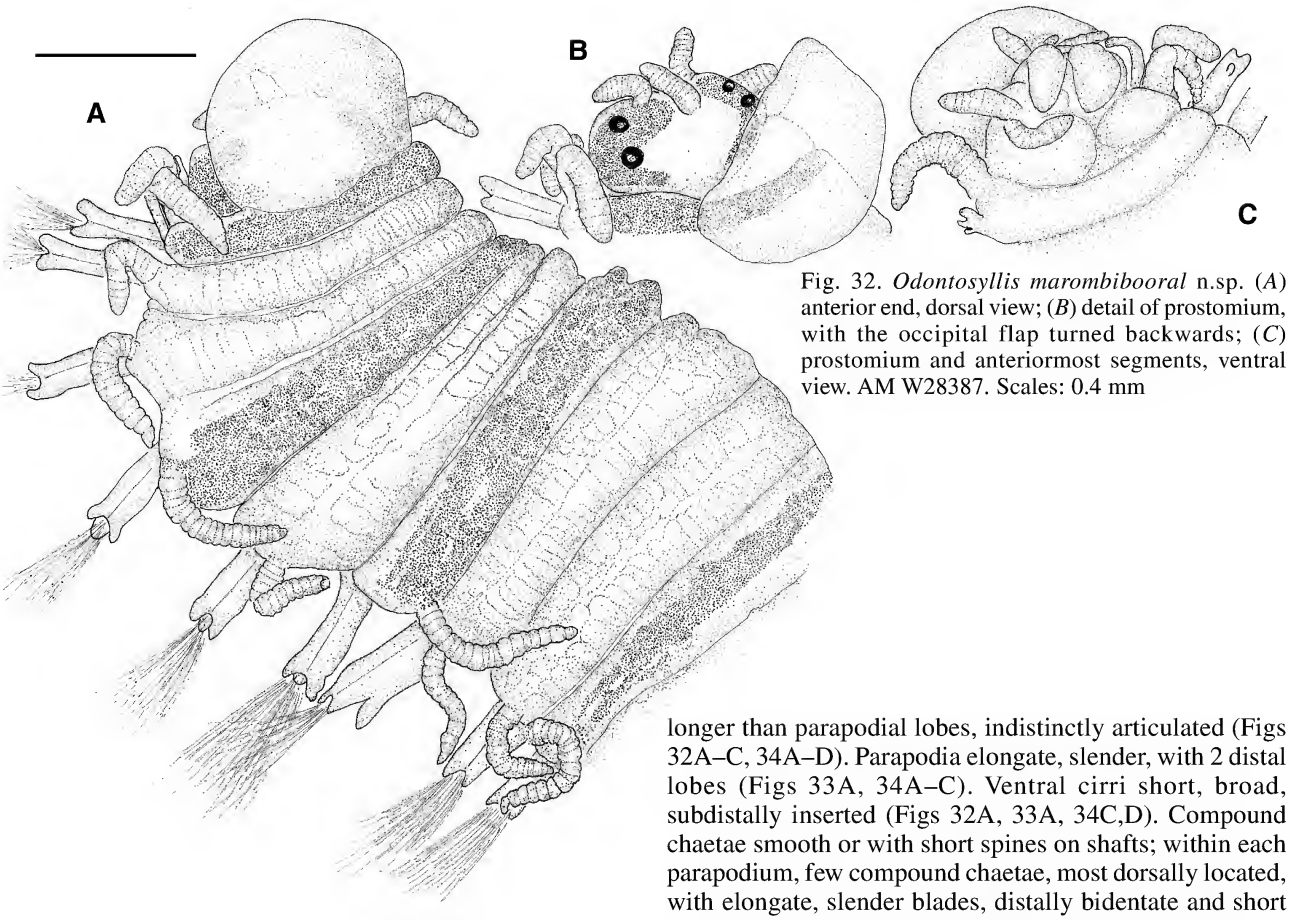


Fig. 32. *Odontosyllis marombibooral* n.sp. (*A*) anterior end, dorsal view; (*B*) detail of prostomium, with the occipital flap turned backwards; (*C*) prostomium and anteriormost segments, ventral view. AM W28387. Scales: 0.4 mm

***Odontosyllis marombibooral* n.sp.**

Figs 23A,B, 32A–C, 33A–F, 34A–E

Material examined. HOLOTYPE (AM W28387) AUSTRALIA: WESTERN AUSTRALIA: Off jetty adjacent to Fisheries Hut, Beacon Is. 28°25.5'S 113°47'E, dead coral substrate, plate-like *Acropora* and *Montipora* spp., 12 m, coll. P.A. Hutchings, 23 May 1994. PARATYPES: 1 on SEM stub (AM W5496) Blow Holes, Quobba, 24°29'S 113°25'E, in sponge, 2 m, coll. N. Coleman, 20 Jun 1972; E side of Mangrove Is. 20°56'S 116°09'E, in dead coral, 1 m, coll. Aquinas College, 9 Jan 1968, 1 (AM W194813).

Description. Body broad, robust anteriorly, tapered posteriorly, 25 mm long, 2 mm wide, with 93 chaetigers. Distinctly coloured (Fig. 32A) with transverse black rows and other yellowish areas on preserved specimens; 2 kidney-shaped black spots on prostomium (Fig. 32B); chaetigers 1, 4, 6, 9 darkly pigmented, subsequent segments, consisting of one darkly pigmented segment followed by unpigmented segment, this striped pattern continues to mid body, following segments with reduced pigmentation; each segment slightly biannulate with dorsum rugose. Prostomium almost circular, totally covered by occipital flap (Figs 32A, 34A,B), with 4 eyes in rectangular pattern, antennae short and thick, shorter than prostomium, indistinctly wrinkled (Fig. 32B,C), originating close to each other, all similar size, median antenna originating slightly posteriorly to lateral antennae, all antennae covered by occipital flap. Palps triangular, ventrally folded (Fig. 32C). Peristomium dorsally reduced, covered by chaetiger 1 and occipital flap (Fig. 32A), forming 2 lobes ventrally (Fig. 32C). Occipital flap large (Figs 32A–C, 34A,B) colourless. Tentacular and dorsal cirri similar, short, thick, slightly longer than parapodial lobes, indistinctly articulated (Figs 32A–C, 34A–D). Parapodia elongate, slender, with 2 distal lobes (Figs 33A, 34A–C). Ventral cirri short, broad, subdistally inserted (Figs 32A, 33A, 34C,D). Compound chaetae smooth or with short spines on shafts; within each parapodium, few compound chaetae, most dorsally located, with elongate, slender blades, distally bidentate and short spines on margin; remaining chaetae with shorter and wider blades that progressively along body, become strongly bidentate, with short spines on margin (Figs 33B,D, 34E, 23A,B). Anterior compound chaetae shorter and more slender than posterior ones, about 20 per parapodium, with dorsoventral gradation in length of blades within fascicle, 38 µm in length dorsally, 16 µm in length ventrally, those of posterior parapodia, numbering about 15 per parapodium, 46 µm in length dorsally, 26 µm in length ventrally. Dorsal and ventral simple chaetae not seen. Aciculae slender, distally broad, numerous on anterior parapodium, numbers decreasing posteriorly to 2–3 on posterior parapodia (Fig. 33C). Pharynx about half of length of proventricle (Fig. 33E), with 5 teeth and 2 lateral plates (Fig. 33F). Proventricle long and wide, with about 56 muscle cell rows (Fig. 33E).

Remarks. *Odontosyllis marombibooral* n.sp. differs from all other species of the genus in having a large occipital flap, which covers totally the prostomium and antennae, a distinctive colour pattern, bifid parapodia with distal ventral cirri, and short, pseudoarticulated dorsal cirri. No other species has this combination of characters. The most similar species is *Odontosyllis picta* (Kinberg, 1865 described as *Eurymedusa picta*), from New Zealand (Ehlers, 1904) (also questionably reported for Australia), which also has a large occipital flap, but not as large as the one present in *Odontosyllis marombibooral* n.sp. *Odontosyllis picta* also has black transverse stripes, but they are arranged in a different pattern to those of *Odontosyllis marombibooral*, and the compound chaetae have all short blades, whereas *Odontosyllis marombibooral*, has two types of chaetae present. *Odontosyllis rubrofasciata* (Pruvot, 1930), from

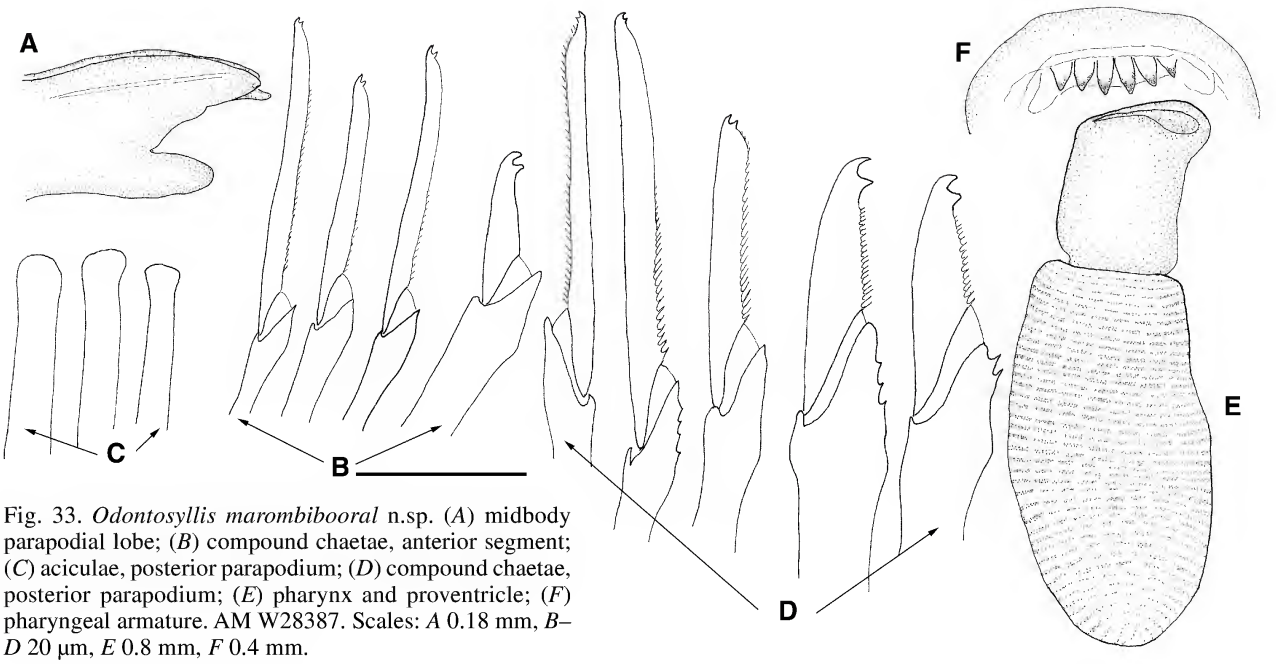


Fig. 33. *Odontosyllis marombibooral* n.sp. (*A*) midbody parapodial lobe; (*B*) compound chaetae, anterior segment; (*C*) aciculae, posterior parapodium; (*D*) compound chaetae, posterior parapodium; (*E*) pharynx and proventricle; (*F*) pharyngeal armature. AM W28387. Scales: *A* 0.18 mm, *B–D* 20 μm, *E* 0.8 mm, *F* 0.4 mm.

New Caledonia, (described as *Atelesyllis rubrofasciata*), and *O. rubrofasciata* Grube, 1878 (a possible homonym), have strikingly similar colour patterns, short dorsal cirri, and compound chaetae that resemble those present in *Odontosyllis marombibooral*, but the occipital flap is much smaller and this character easily separates these three species. Fauvel, in the notes given after the description of *Atelesyllis rubrofasciata* considered that is a different species to *O. rubrofasciata* Grube, 1879. *Odontosyllis rubrofasciata* (Pruvot, 1930) has transverse stripes, but only from the midbody onwards, the prostomium has 4 lobes. The chaetae, although similar to those of *O. marombibooral* are slightly different, with long blades not as elongated and short blades with distal tooth not as curved as those present in *O. marombibooral*. In the description of *Atelesyllis rubrofasciata* (Pruvot, 1930), pharyngeal teeth are not mentioned as being present, although examining a range of species of *Odontosyllis* some individuals appear to lack these teeth. In all other characters, however, they are identical to specimens with teeth, suggesting they may lose these teeth and be able to regenerate them.

Habitat. Occurring in dead corals and sponges, from depths of 1–12 m.

Distribution. Australia (Western Australia).

Etymology. The name of this species comes from two aboriginal words, *marombi*, meaning shield, and *booral*, meaning big, or large, in reference to the large occipital flap present.

Odontosyllis polycera (Schmarda, 1861)

Figs 19A,B, 25E,F, 35A–F, 36A–F

Syllis polycera Schmarda, 1861: 72, pl. 28, fig. 219
Odontosyllis polycera Augener, 1927: 152.—Day, 1967: 260, fig. 12.—Hutchings & Murray, 1984: 32.—Hartmann-Schröder, 1984: 20; 1985: 68, figs 14–17; 1986: 41; 1989: 25; 1990: 51.
?*Odontosyllis suteri* Non Benham, 1915.—Haswell, 1920: 107.

Material examined. AUSTRALIA: QUEENSLAND: Lagoon, Low Islets, 16°23'S 145°34'E, British Great Barrier Reef Expedition 1928–1929, 3 Oct 1928, id. as *O. hyalina*, 1 epigamic specimen, (AM W2952). NEW SOUTH WALES: NE of Mary's Rock, Cook Is., 28°11.42'S 153°34.79'E, orange frilly bryozoan, 19 m, coll. R.T. Springthorpe, 8 Jun 1993, 1 (AM W28400); NW of Split Solitary Is., 30°14'S 153°10.8'E, orange sponge, 14 m, coll. R.T. Springthorpe, 7 Mar 1992, 1 (AM W28219); Green Point, Hawkesbury R., 33°34'S 151°14'E, mud, 12 m, coll. A. Jones & party, 13 Nov 1979, 1 (AM W196605); Hawkesbury R., E end of Brooklyn Boat Channel, 33°33'S 151°14'E. A. Jones & party, 18 Dec 1979, 1 (AM W196420); Grotto Point, Port Jackson, 33°49'S 151°15'E, algae, 4 m, coll. P. Colman, 18 July 1983, 2 (AM W28407); W of La Perouse, Botany Bay, 33°59.4'S 151°12.8'E, St. 99, mud, 13 m, coll. SPCC, 10 Mar 1977, P.A. Hutchings (id.), 1 epigamic female, (+ 2 midbody pieces on SEM stub) (AM W14203); S of Banksmeadow, Botany Bay, 33°58'S 151°12'E, mud, 19 m, 8 Dec 1976, coll. SPPC, 1 (AM W14197); Botany Bay, 33°59.3'S 151°13.1'E, coll. NSW Fisheries, 31 Jan 1975, 1 epigamic specimen on SEM stub (AM W195387); Botany Bay, 34°0.5'S 151°11'E, coll. NSW Fisheries, 1 (AM W195520); N of Kurnell, Botany Bay, 34°00'S 151°12'E, mud, 13 m, 10 March 1977, P.A. Hutchings (id.), 1 (AM W14204); Port Botany, Botany Bay, 33°58.75'S 151°11.093'E, 7 m, 7 Apr 1992, A. Murray (id.), 1 (AM W21628); W of La Perouse, Botany Bay, muddy sand, 19 m, 4 Feb 1977, coll. SPCC, 2 (AM W14201); off Bass Point, 34°36'S 150°54'E, 50 m, coll. The Ecology Lab, 1 Feb 1990, several (AM W22990); 100 m, Jervis Bay, 35°06'S 150°44'E, coll. P.A. Hutchings & party, Feb 1989, 1 (AM W20828); Jervis Bay, off Murrays Beach, 35°7.5'S 150°45.5'E, coll. NSW Fisheries, 25 Apr 1972, 1 on SEM stub (AM W194258); Jervis Bay, Murrays Basin sandbank, coll. NSW Fisheries, 17 Oct 1972, 1 (AM W194540); Jervis Bay, Murrays Basin 35°7.5'S 150°45.5E, sand, coll. NSW Fisheries, 17 Oct 1972, 1 (AM W194290); Jervis Bay, off Murrays Beach, 35°7.5'S 150°45.5'E, NSW Fisheries, Apr 1972, 1 (AM W17559); Plantation Point, Jervis Bay, 35°4.35'S 150°41.80'E, intertidal rock platform, coll. A. Murray, 24 Oct 1998, 1 (AM W24937). TASMANIA: Fancy Point, Bruny Is. 43°16'S 147°19'E, algae, 3–6 m, coll. G. Edgar, 10 Nov 1980, 1 (AM W18189). SOUTH AUSTRALIA: 2 km off First Creek, Spencer Gulf, Port Pirie, 33°12'S 138°00'E, subtidal, *Posidonia* and *Amphibolus* spp seagrass, 4.1 m, T.J. Ward, Mar 1980, 1 (AM W28233); Sleaford Bay, Port Lincoln, 34°54'S 135°47'E, algal washings, coll. P.A. Hutchings, 10 Mar 1979, 4 (AM W26356). WESTERN AUSTRALIA: Bramble Point, Princess Royal Harbour, 35°02'S 117°55'E, *Posidonia sinuosa*, 1–1.5m, coll. P.A. Hutchings & party, Jan 1988, 1 (AM W20305); Cottlesloe Beach, 6 miles W of Perth, calcareous algae & *Idanthyrsus* tubes, 6 m, coll. H. Paxton, 14 Feb 1970, G. Hartmann-Schröder (id.), 6 (+ 2 fragments on SEM stub), (AM W4344); Red Bluff, Kalbarri, 27°42'S 114°09'E, mixed coralline algae on rocky shore, 3.5 m, coll. J.K. Lowry, 10 Jan., 1984, 2 (AM W28365).

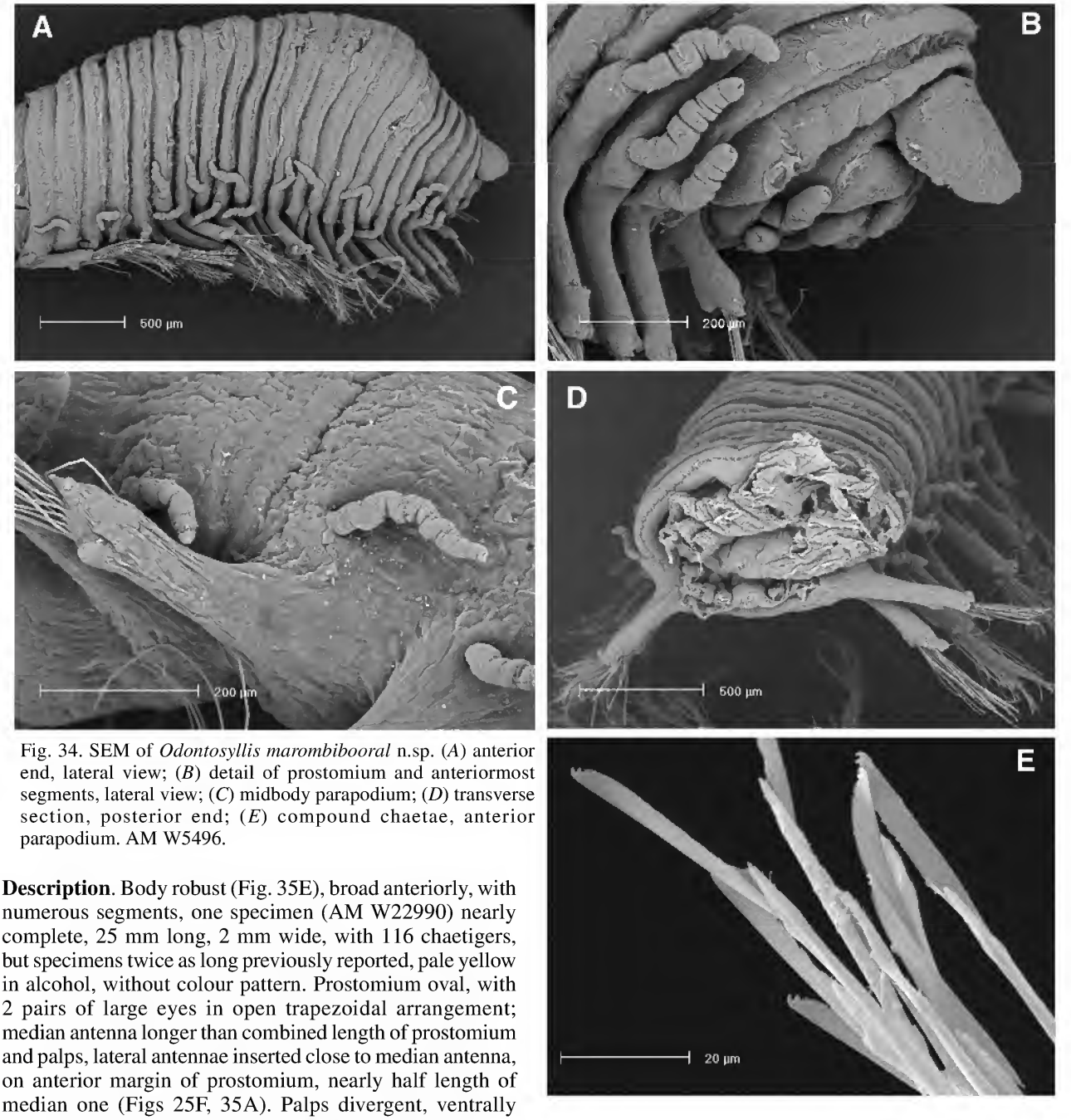


Fig. 34. SEM of *Odontosyllis marombibooral* n.sp. (*A*) anterior end, lateral view; (*B*) detail of prostomium and anteriormost segments, lateral view; (*C*) midbody parapodium; (*D*) transverse section, posterior end; (*E*) compound chaetae, anterior parapodium. AM W5496.

Description. Body robust (Fig. 35E), broad anteriorly, with numerous segments, one specimen (AM W22990) nearly complete, 25 mm long, 2 mm wide, with 116 chaetigers, but specimens twice as long previously reported, pale yellow in alcohol, without colour pattern. Prostomium oval, with 2 pairs of large eyes in open trapezoidal arrangement; median antenna longer than combined length of prostomium and palps, lateral antennae inserted close to median antenna, on anterior margin of prostomium, nearly half length of median one (Figs 25F, 35A). Palps divergent, ventrally folded, free for almost their length, fused basally. Dorsal tentacular cirri slightly longer than antennae, ventral tentacular cirri shorter. Peristomium reduced dorsally, covered by large, long occipital flap, that also covers most of prostomium (Figs 25E,F, 35A); anterior edge of occipital flap with band of cilia (Fig. 36A, arrow); midbody segments divided in two sections by one furrow, each section with row of cilia (Fig. 36B, arrows). Antennae, tentacular, and dorsal cirri elongated, smooth, distally tapered, with short cirrophore (Figs 25E, 35A), dorsal cirri becoming shorter posteriorly (Fig. 25E); dorsal cirri of chaetigers 1, 3, 4 and 6 long, alternating dorsal cirri long and short on remaining segments. Parapodia conical, ending in 2 distal lobes (Fig. 35B). Ventral cirri rounded, stout, pillow-shaped, shorter than parapodial lobes (Figs 35B, 36C,D). Compound chaetae heterogomph falcigers, with spinose ending shafts and short, bidentate blades, slightly hooked, proximal tooth well separated from distal ones (Figs 35E,F, 36F), sometimes on middle of margin; few, short spines, on margin, also some thin spines on tendons between shafts and blades, becoming more marked on posterior chaetae (Fig. 35E,F). Length of blades of chaetae within fascicle increasing ventrally (Figs 35E,F, 36E). Anterior parapodia with about 50 compound chaetae, blades 15–17 µm in length dorsally, 23 µm in length ventrally; number of compound chaetae per parapodium diminishing progressively along body to 25–27 on posterior segments, blades increasing in length within fascicle from 18 µm dorsally to 25 µm ventrally. Anterior parapodia with 3 slender aciculae with trilobed tips, numbers decreasing posteriorly with only 1 on posterior parapodia, similar to anterior ones (Fig. 35D), but larger. Dorsal simple chaetae on posterior parapodia, thin, unidentate, with short spines on margin (Fig. 19A).

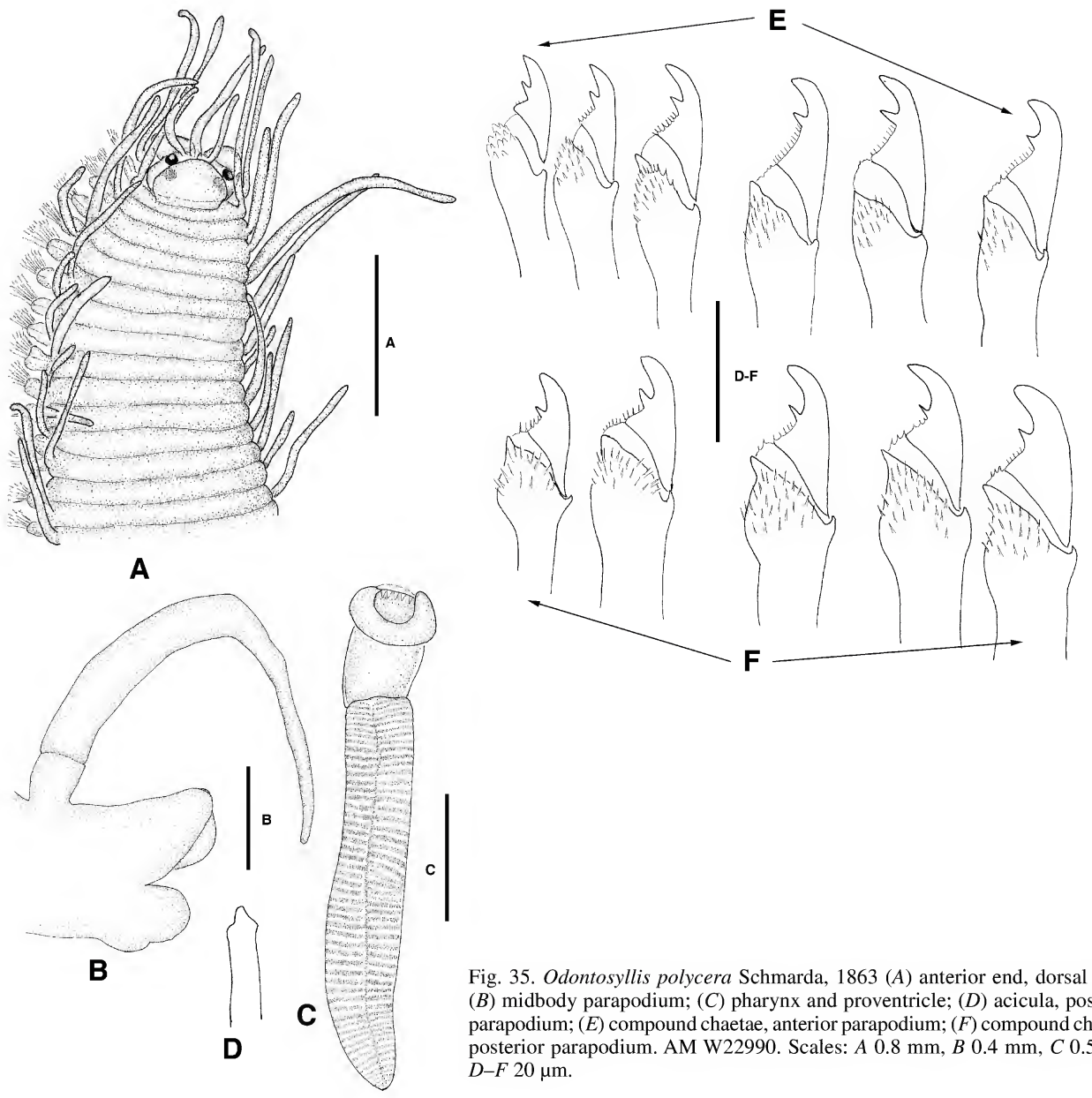


Fig. 35. *Odontosyllis polycera* Schmarda, 1863 (*A*) anterior end, dorsal view; (*B*) midbody parapodium; (*C*) pharynx and proventricle; (*D*) acicula, posterior parapodium; (*E*) compound chaetae, anterior parapodium; (*F*) compound chaetae, posterior parapodium. AM W22990. Scales: *A* 0.8 mm, *B* 0.4 mm, *C* 0.5 mm, *D–F* 20 μm.

Ventral simple chaetae on far posterior segments of few specimens, with minute subdistal spines on margin, distally hooked, with short proximal tooth (Fig. 19B). Pharynx short, through about 4 segments, with 5–8 teeth, and 2 lateral plates. Proventricle long, relatively slender, more than 3 times length of pharynx (Fig. 35C), through 9–10 segments, with about 130 muscle cell rows. Pygidium, with 2 long anal cirri. Several specimens epitokous, with long natatory chaetae on midbody parapodia (Fig. 36D).

Remarks. This species, which was described from Table Bay, South Africa, has been reported widely, and a detailed study should be undertaken to confirm such a wide distribution and depth range.

Habitat. Occurring in sand, mud, algae, calcareous substrata, bryozoans, sponges, from intertidal to 90 m (Hartmann-Schröder, 1984).

Distribution. Angola, Namibia, South Africa, USA (Southern California), Panama, Indo-Pacific, New Zealand, Australia (Queensland, New South Wales, Tasmania, South Australia, Western Australia).

Genus *Opisthodonta* Langerhans, 1879

Opisthodonta Langerhans, 1879: 547.

Type species. *Opisthodonta morena* Langerhans, 1879.

Diagnosis. Body long, with numerous segments, stout, dorsally convex, of macrofaunal size (>10 mm in length). Prostomium provided with 2 pairs of eyes, and sometimes 2 anterior eyespots. Three antennae. Median antenna

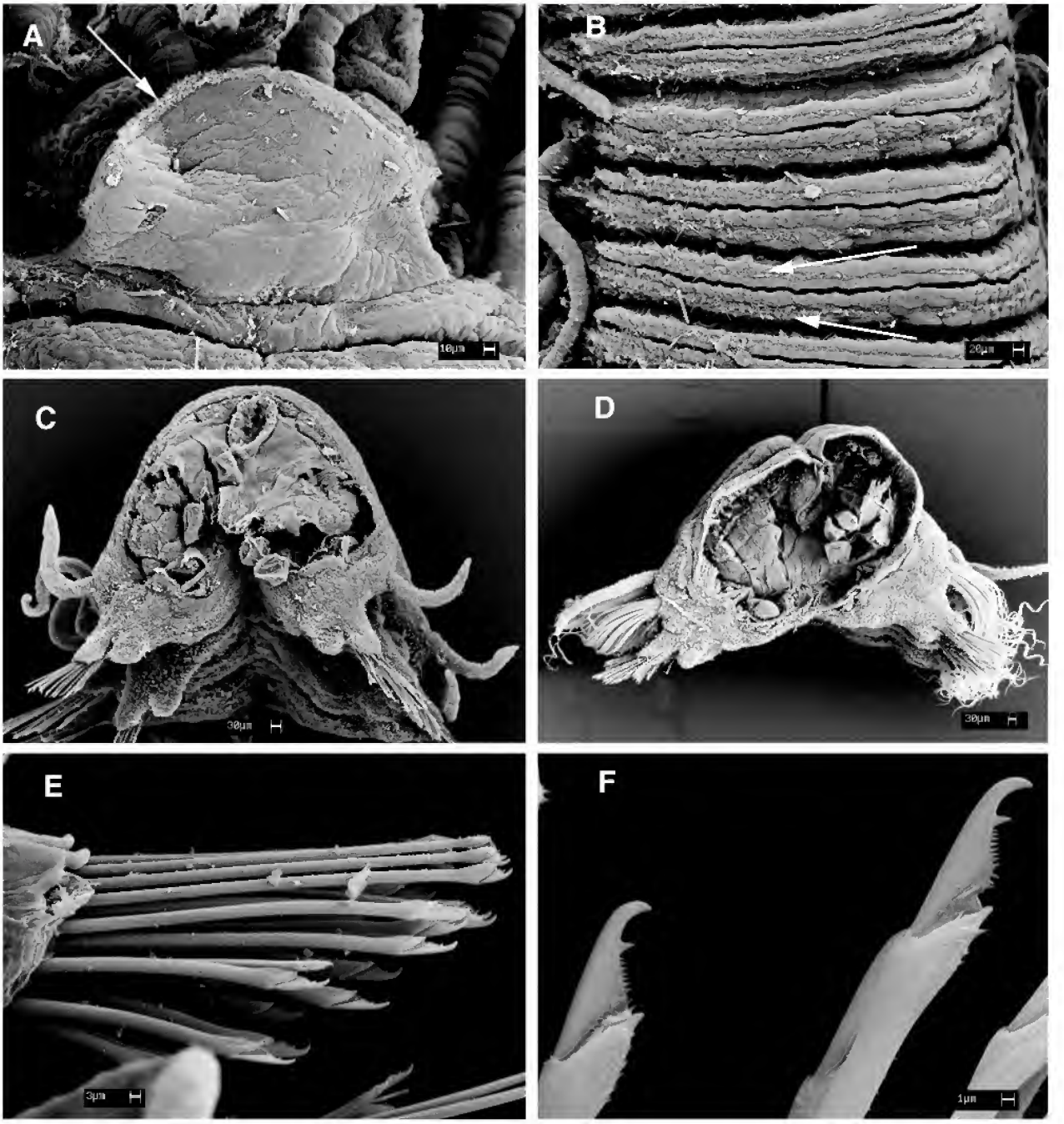


Fig. 36. SEM of *Odontosyllis polycera* Schmarda, 1863 (*A*) occipital flap; (*B*) detail of dorsum of midbody segments; (*C*) transverse section, midbody of an atokous specimen; (*D*) transverse section, midbody of an epigamic specimen; (*E*) fascicle of chaetae, midbody; (*F*) compound chaetae, midbody. *A,B*: AM W195387; *C*: AM W4344; *D*: AM W14203; *E,F*: AM W4344.

inserted on middle of prostomium or slightly in front of anterior eyes. Palps apparently free from each other, basally fused. Peristomium small, partially covered by prostomium and first chaetiger, with 2 pairs of tentacular cirri. Nuchal organs as 2 ciliated grooves between prostomium and peristomium. Dorsal cirri on all chaetigers, cylindrical, long to extremely long, smooth or slightly rugose. Parapodia elongate; ventral cirri of anterior parapodia, ovate, foliaceous almost completely fused with parapodial lobe, provided with hyaline inclusions, perhaps glands. Subsequent ventral cirri conical to digitiform, neither foliaceous nor fused to parapodial lobes, inserted at base of parapodia. Chaetal bundles formed of numerous compound chaetae, including falcigers provided with long, thick proximal tooth and short distal tooth and sometimes a few chaetae with long, slender, spiniger-like blades. Dorsal simple chaetae apparently lacking. Aciculae with button-shaped tips with crown of spines, or tricuspidate. Pharynx and proventricle similar in length. Pharynx with crown of soft papillae on anterior rim and single mid-dorsal tooth, inserted on anterior third or middle of pharynx. Reproduction by epigamy (Garwood, 1991).

Key to Australian species of *Opisthodonta*

1 Pharyngeal tooth inserted mid to far posterior of pharynx. Spiniger-like chaetae absent ..... *O. morena*

—— Pharyngeal tooth located in front of middle of pharynx. Spiniger-like chaetae present 2

2 Spiniger-like chaetae about 84 µm in midbody, bidentate. Dark, transverse rows of pigment on anterior segments ..... *O. melaenonephra*

—— Spiniger-like chaetae about 175 µm in midbody, weakly bidentate to unidentate. Lacking any colour pattern ..... *O. hanneloreae* n.sp.

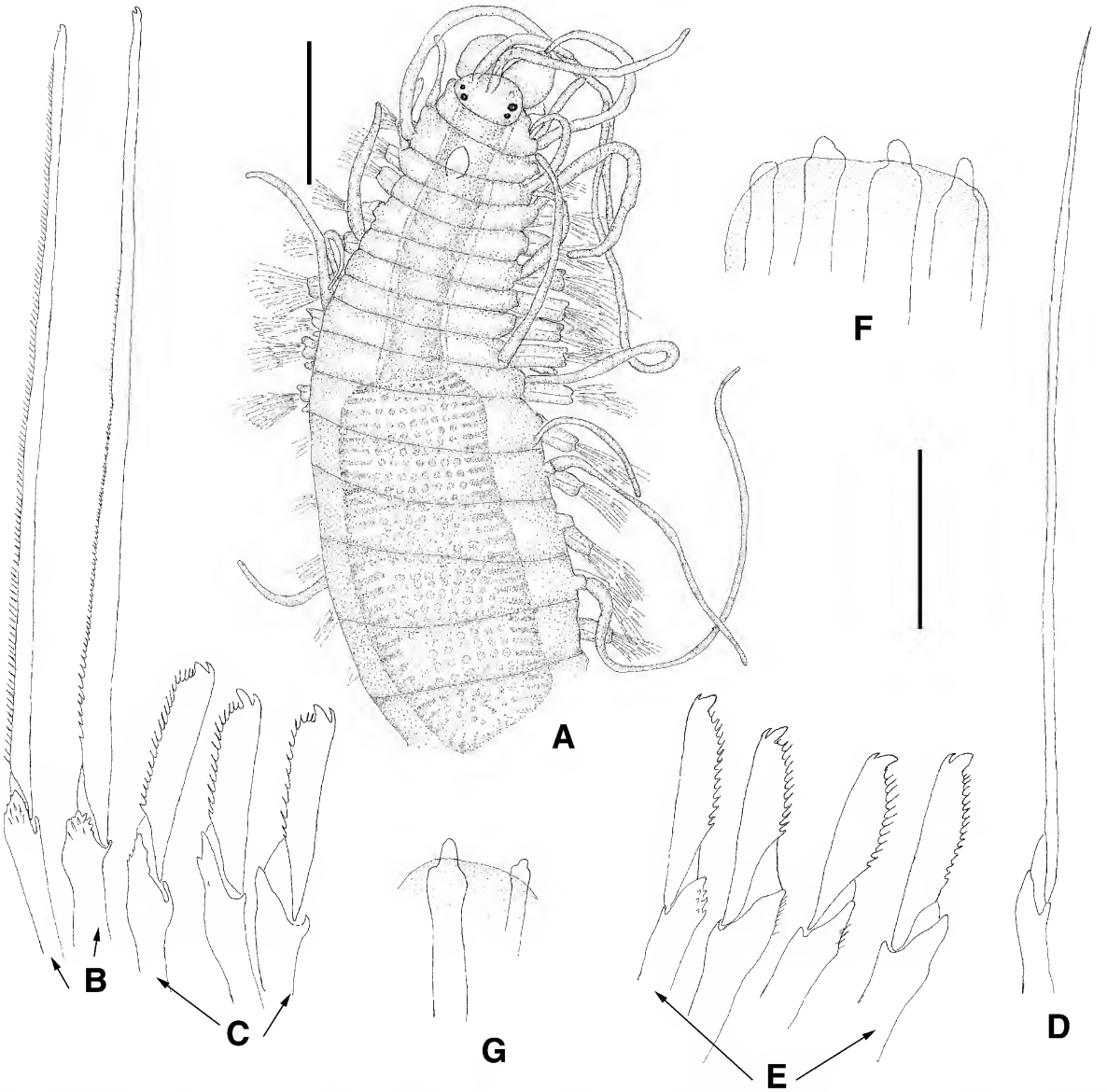


Fig. 37. *Opisthodonta hanneloreae* n.sp. (*A*) anterior end, dorsal view; (*B*) spiniger-like compound chaetae, anterior parapodium; (*C*) falcigers, anterior parapodium; (*D*) spiniger-like compound chaeta, midbody; (*E*) falcigers, midbody; (*F*) aciculae, anterior parapodium; (*G*) aciculae, midbody. AM W28393. Scales: *A* 0.18 mm, *B–G* 20 µm.

Opisthodonta hanneloreae n.sp.

Fig. 37A–G

Material examined. HOLOTYPE (AM W28393). AUSTRALIA: WESTERN AUSTRALIA: Wallabi Group of Is., 28°23.99'S 113°46.73'E, shell debris from scallop beds, 39 m, coll. P.A. Hutchings on WA FRV *Flinders*, 30 May 1994. PARATYPES Wallabi Group of Is., 28°24'S 113°46.26'E, scallop beds, shell debris, 35 m, coll. P.A. Hutchings on WA FRV *Flinders*, 30 May 1994, few (AM W28372); Off S end of Long Is. Beacon Is. 28°28.8'S 113°46.3'E, dead coral substrate covered in coralline algae, 4.5 m, coll. P.A. Hutchings, 25 May 1994, 1 (AM W28950); Goss Passage, Beacon Is. 28°25.5'S 113°47'E, dead coral substrate, in fine sediment at foot of reef slope, 33 m, coll. P.A. Hutchings, 23 May 1994, 1 (AM W28951).

Description. Body fragile, all fragmented specimens, strongly convex dorsally, colourless, longest anterior fragment 2.8 mm long, 0.6 mm wide, with 18 chaetigers. Prostomium oval, with 4 eyes in open trapezoidal arrangement and sometimes 2 anterior eyespots; median antenna inserted in front of line between anterior eyes, about twice as long as combined length of prostomium and palps; lateral antennae inserted near anterior margin, about half length of median antenna (Fig. 37A). Palps trapezoidal, sometimes ventrally folded, slightly longer than prostomium. Peristomium similar in length to following segments; dorsal tentacular cirri long, filiform, longer than median antenna, ventral tentacular cirri about one third length of dorsal cirri. Dorsal cirri, as well as antennae and tentacular cirri, smooth, filiform, alternating irregularly, long cirri, longer than body width, and short cirri, shorter than body width (Fig. 37A). Parapodial lobes rectangular, ending with pre-chaetal lobe. Ventral cirri large, triangular, partially fused to parapodial lobes on anterior parapodia, with some granular inclusions, becoming digitiform, not fused to parapodial lobes, on subsequent segments. Compound chaetae compound heterogomph, shafts distally spinose, and two kinds of blades, long, spiniger-like chaetae, anteriorly bifid (Fig. 37B), apparently unidentate on posterior parapodia (Fig. 37D), and bidentate falcigers, elongate, with short spines on margin and margins of blades weakly convex on anterior parapodia, bidentate, with unequal teeth, proximal tooth longer and broader than distal tooth (Fig. 37C), becoming more marked on posterior chaetae (Fig. 37E). Anterior parapodia with about 3 spiniger-like chaetae, blades 90–175 µm in length; and about 50 falcigers with blades 25–27 µm in length; progressively posteriorly number of compound chaetae decreasing to 1–2 spiniger-like, about 105 µm in length, smooth and unidentate, and 25 falcigers, 25–22 µm in length, on mid-posterior parapodia. Simple dorsal and ventral chaetae not seen. Aciculae distally slightly enlarged, ending in button, 4 on most anterior parapodia (Fig. 37F), reducing to 2 on mid-posterior parapodia, one large and other slender (Fig. 37G). Pharynx long and slender, through about 11 segments; pharyngeal tooth long and large, oval, located slightly anteriorly to middle of pharynx (Fig. 37A). Proventricle large, through about 6 segments, with 23 muscle cell rows. Details of posterior end unknown.

Remarks. *Opisthodontha hanneloreae* n.sp. is similar to *O. melaenonephra*, but lacks any colour pattern, the spiniger-like chaetae are distinctly longer and more slender, unidentate from midbody onwards. *Opisthodonta morena* Langerhans, 1879 (see above), and *O. mitchelli* Kudenov & Harris (1995) have much shorter spiniger-like chaetae than *O. hanneloreae*.

Habitat. Occurring in dead corals and in shell debris, in shallow water.

Distribution. Australia (Western Australia).

Etymology. The species is named after Dr Hannelore Paxton an Australian polychaetologist.

Opisthodonta melaenonephra (Haswell, 1920) n.comb.

Figs 38A–G, 39A–O

Pionosyllis melaenonephra Haswell, 1920: 103, pl. 12, figs 11–16, pl. 13, fig. 1.—Hutchings & Murray, 1984: 32.

Material examined. AUSTRALIA: NEW SOUTH WALES: Offshore from Hungry Beach, Hawkesbury R., 33°35'S 151°17'E, sandy mud, 4 m, coll. A.R. Jones & A. Murray, 9 Nov 1982, 2 (AM W22122); Offshore from Hungry Beach, Hawkesbury R., 33°35'S 151°17'E, sandy mud, 4 m, coll. A.R. Jones & A. Murray, 5 Aug 1983, 1 (AM W22123); Offshore from Hungry Beach, Hawkesbury R., 33°35'S 151°17'E, sandy mud, 4 m, coll. A.R. Jones & A. Murray, 11 Nov 1983, 1 (AM W22124); Offshore from Hungry Beach, Hawkesbury R., 33°35'S 151°17'E, sandy mud, 4 m, coll. A.R. Jones & A. Murray, 17 May 1982, 1 (AM W22126); Offshore from Hungry Beach, Hawkesbury R., 33°35'S 151°17'E, sandy mud, 4 m, A.R. Jones & A. Murray, 26 May 1981, 1 (AM W22127); Offshore from Hungry Beach, Hawkesbury R., 33°35'S 151°17'E, sandy mud, 4 m, coll. A.R. Jones & A. Murray, 9 Nov 1982, 1 (AM W22128); mid-stream between Juno Head and Hungry Beach, Hawkesbury R., 33°34'S 151°16'E, muddy sand, 10 m, coll. A.R. Jones & A. Murray, 9 Nov 1984, 1 (AM W22129); 50 m NE of Green Point, Hawkesbury R., 33°34'S 151°13.5'E, muddy sand, 4 m, coll. A.R. Jones & A. Murray, 9 Nov 1982, 1 (AM W22131); 50 m NE of Green Point, Hawkesbury R., 33°34'S 151°13.5'E, muddy sand, 4 m, coll. A.R. Jones & A. Murray, 5 Aug 1983, 2 (AM W22132); 300 m NE of Green Point, Hawkesbury R., 33°34'S 151°13.5'E, sandy mud, 5 m, coll. A.R. Jones & A. Murray, 26 May 1981, 1 (AM W22133); 300 m NE of Green Point, Hawkesbury R., 33°34'S 151°13.5'E, sandy mud, 5 m, coll. A.R. Jones & A. Murray, 7 Aug 1981, 1 (AM W22134); 300 m NE of Green Point, Hawkesbury R., 33°34'S 151°13.5'E, sandy mud, 5 m, coll. A.R. Jones & A. Murray, 26 May 1981, 1 (AM W22135); 300 m NE of Green Point, Hawkesbury R., New South Wales, Australia, 33°34'S 151°13.5'E, sandy mud, 5 m, coll. A.R. Jones & A. Murray, 11 Nov 1983, 1 (AM W22136); 1 km S of E end of Spectacle Is., Hawkesbury R., 33°32'S 151°07.5'E, muddy sand, 12 m, coll. A.R. Jones & A. Murray, 5 Aug 1983, 1 (AM W22138); 1 km S of E end of Spectacle Is., Hawkesbury R., 33°32'S 151°07.5'E, muddy sand, 12 m, coll. A.R. Jones & A. Murray, 21 Aug 1984, 1 (AM W22139); 300 m NE of Green Point, Hawkesbury R., 33°34'S 151°13.5'E, sandy mud, 5 m, coll. A.R. Jones & A. Murray, 4 Feb 1983, 1 (AM W22140); 300 m NE of Green Point, Hawkesbury R., 33°34'S 151°13.5'E, sandy mud, 5 m, coll. A.R. Jones & A. Murray, 11 Feb 1981, 1 (AM W22141); 300 m NE of Green Point, Hawkesbury R., 33°34'S 151°13.5'E, sandy mud, 5 m, coll. A.R. Jones & A. Murray, 27 May 1983, 1 (AM W22142); 300 m NE of Green Point, Hawkesbury R., 33°34'S 151°13.5'E, sandy mud, 5 m, coll. A.R. Jones & A. Murray, 11 Feb 1981, 3 (AM W22143); 300 m NE of Green Point, Hawkesbury R., 33°34'S 151°13.5'E, sandy mud, 5 m, coll. A.R. Jones & A. Murray, 7 Aug 1981, 1 (AM W22144); 300 m NE of Green Point, Hawkesbury R., 33°34'S 151°13.5'E, sandy mud, 5 m, coll. A.R. Jones & A. Murray, 7 Aug 1981, 1 (AM W22145); 1 km S of E end of Spectacle Is., Hawkesbury R., 33°32'S 151°07.5'E, muddy sand, 12 m, coll. A.R. Jones & A. Murray, 9 Feb 1984, 1 (AM W22147); 1 km S of E end of Spectacle Is., Hawkesbury R., 33°32'S 151°07.5'E, muddy sand, 12 m, coll. A.R. Jones & A. Murray, 21 Aug 1984, 1 (AM W22148); E end of Brooklyn Boat Channel, Hawkesbury R., 33°33'S 151°14'E, 12 m, coll. A. Jones *et al.*, 18 Dec 1979, 1 (AM W196608). E end of Brooklyn Boat Channel, Hawkesbury R., 33°33'S 151°14'E, A. Jones *et al.*, 1 Aug 1979, 5 (AM W196610); 200 m S of E end of Spectacle Is., Hawkesbury R., 33°32.5'S 151°13.5'E, sandy mud, 5 m, coll. A.R. Jones & A. Murray, 11 Nov 1983, 1 (AM W22150). Pittwater, 33°35.87'S 151°18.71'E, mud, 15.9 m, coll. Australian Museum Party, 15 Dec 1994, 1 (AM W23929); Port Jackson, 33°51'S 151°16'E, Feb 1920. Syntypes: Port Jackson, 33°51'S 151°16'E, Feb 1920, 2 (AM W513), 8 (AM W6175), 1 on microscope slide (AM W494). Rock platform, Murray's Beach, Jervis Bay, 35°07.5'S 150°46'E, dead barnacles encrusted with sponges, in intertidal pools, 0.5 m, coll. H.E. Stoddart, 28 Jun 1981, 1 (AM W28412); Summercloud Bay, Jervis Bay, 35°10.4'S 150°41.2'E, 15.8 m, coll. P.A. Hutchings, 29 Nov 1971, 1 (AM W28435); Murrays Basin, Jervis Bay, 35°07.5'S 150°45.5'E, sand, *Zostera* sp., coll. NSW State Fisheries, 17 Oct 1972, 1 (AM W194168).

Description. Body long (>10 mm in length) and broad, fragile, strongly convex dorsally, dark, 1–3 transverse dark bands on dorsum of anterior segments, as well as two black

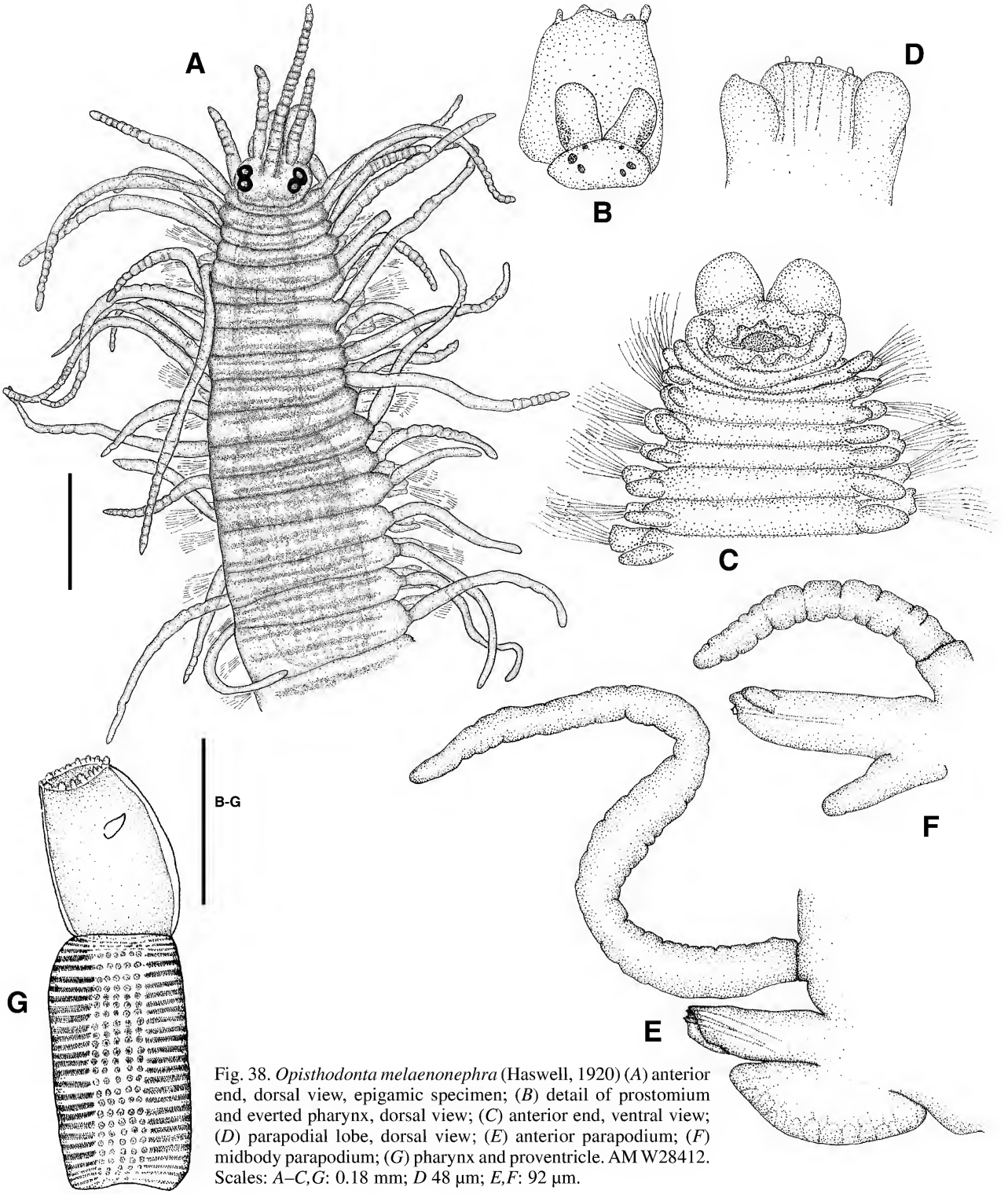


Fig. 38. *Opisthodonta melaenonephra* (Haswell, 1920) (*A*) anterior end, dorsal view, epigamic specimen; (*B*) detail of prostomium and everted pharynx, dorsal view; (*C*) anterior end, ventral view; (*D*) parapodial lobe, dorsal view; (*E*) anterior parapodium; (*F*) midbody parapodium; (*G*) pharynx and proventricle. AM W28412. Scales: *A–C,G*: 0.18 mm; *D* 48 µm; *E,F*: 92 µm.

spots on each palp, with dark pigment on prostomium; one epigamic specimen (AM W28412) with this pattern well developed (Fig. 38A), but others less pigmented. (Haswell recorded an individual 14 mm long, 1 mm wide for 65–75 segments). Prostomium ovate with 4 eyes arranged in open trapezoidal pattern and, sometimes 2 small anterior eyespots. Median antenna long, inserted on middle of prostomium, between anterior eyes, slightly longer than twice combined length of prostomium and palps; lateral antennae shorter, about half of median antenna, arising in front of anterior pair of eyes (Fig. 38A). Palps apparently basally free, ovate (Fig. 38B), sometimes ventrally folded. Dorsal tentacular cirri similar in length to median antenna, ventral tentacular cirri similar to lateral antennae. Antennae, tentacular cirri and dorsal cirri long, slender, cylindrical, smooth on midbody and posterior segments, to rugose, not articulated, supported by short cirrophores or indistinctly articulated on antennae, dorsal tentacular cirri and most anterior dorsal cirri (Fig. 38A,E). Dorsal cirri alternating, twice as long as body width on most anterior segments, and short, similar

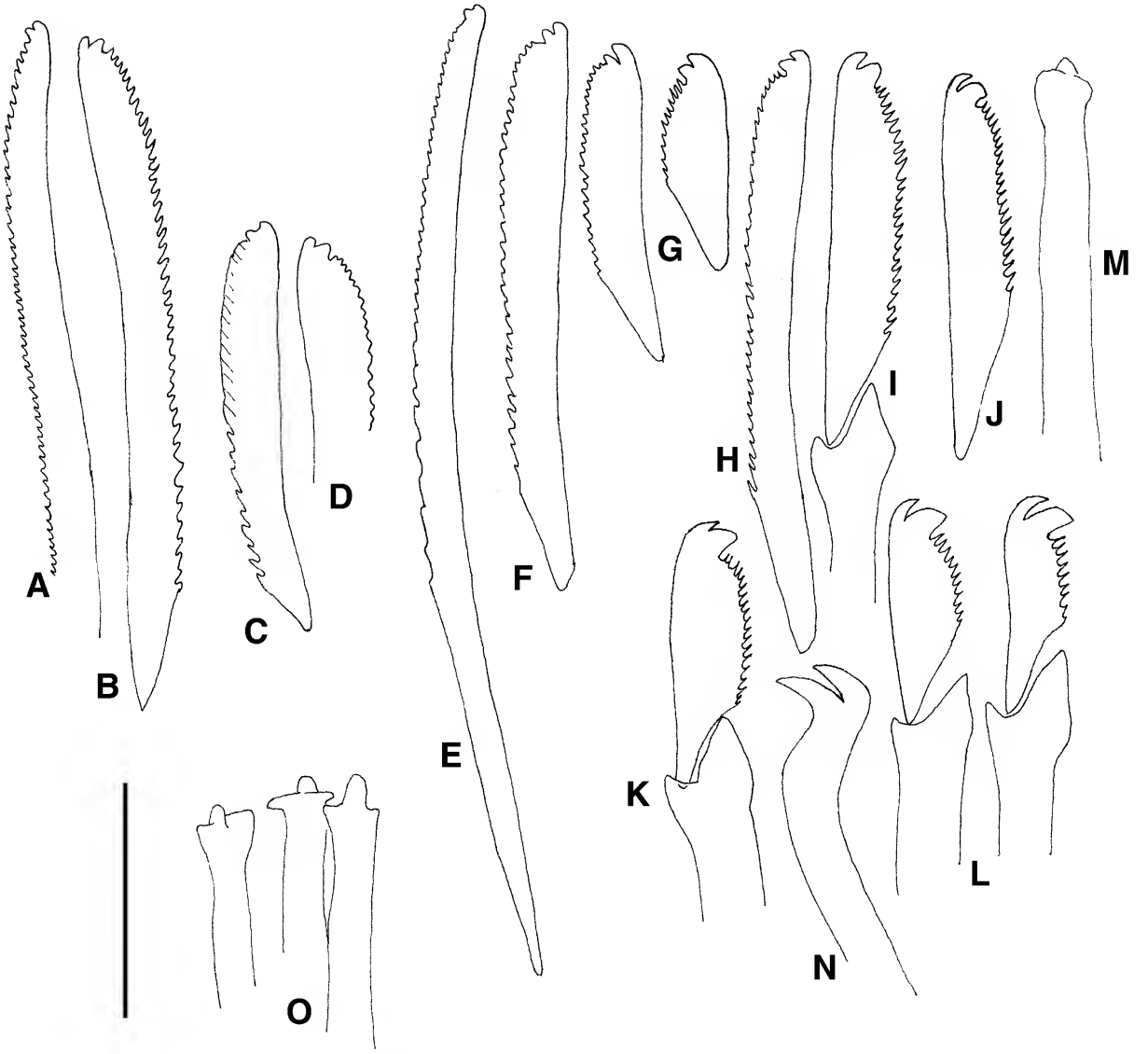


Fig. 39. *Opisthodonta melaenonephra* (Haswell, 1920) (*A*) distal end of spiniger-like chaeta, anterior parapodium; (*B*) blade of spiniger-like chaeta, anterior parapodium; (*C,D*) blades of falcigers, anterior parapodium; (*E*) spiniger-like chaeta, midbody; (*F,G*) blades of falcigers, midbody; (*H*) spiniger-like blade, posterior parapodium; (*I–L*) blades and falcigers, posterior parapodium; (*M*) acicula, posterior parapodium; (*N*) ventral simple chaeta; (*O*) aciculae, anterior parapodium. AM W494. Scales: 20 μm.

in length to body width. Parapodia slender, elongate, subrectangular, with 2 rounded lobes on anterodorsal and posterodorsal margins of parapodia (Fig. 38D). Ventral cirri of anterior parapodia foliaceous, thick, partially fused to base of parapodial lobe, with hyaline inclusions near ventral surface (Fig. 38E), becoming progressively shorter, not fused to parapodial lobe, digitiform (Fig. 38F). Anterior parapodia, except those of 2–3 most anterior segments, with 2–3 compound chaetae with long, slender, spiniger-like blades, about 125 μm long, indistinctly bifid distally (Fig. 39A,B), with proximal tooth slightly larger than distal tooth and short, indistinct spines on margin, and about 15 compound falcigerous chaetae, with elongate, bidentate blades provided with short and slightly hooked distal tooth (Fig. 39C,D), larger and triangular proximal tooth, and short, straight spines on margin; dorsoventral gradation in length of blades within fascicle, 65 μm in length dorsally, 25 μm in length ventrally, ventral blades larger with marked difference in size of teeth (Fig. 39E–G); blades with margins weakly convex, becoming more marked ventrally within fascicle. Posteriorly, blades of spiniger-like chaetae becoming progressively shorter, and falcigers with wider blades; posterior parapodia with single compound chaetae with elongate, spiniger-like blade (Fig. 39H), about 60 μm in length, and 3–4 chaetae with falcigerous blades with dorsoventral gradation in length within fascicle, 50 μm in length dorsally, 25 μm in length ventrally; spiniger-like blade with margins weakly convex and distally bidentate, with both teeth almost equal (Fig. 39I–L). Dorsal simple chaetae not seen, probably absent. Ventral simple chaetae only seen on far posterior parapodia of holotype, sigmoid, stout, strongly bidentate, bearing proximal tooth longer than distal tooth (Fig. 39N). Anterior parapodia with 3 tricuspidate tipped aciculae (Fig. 39 O) remaining parapodia, except posteriormost ones, with 2 similar aciculae. Posteriormost parapodia, each with single acicula, tip distally rounded, with button (Fig. 39M). Pharynx short and wide, extending through about 7–8 segments, with crown of about 16 soft papillae; pharyngeal tooth conical, large, located just in front of middle of pharynx (Fig.

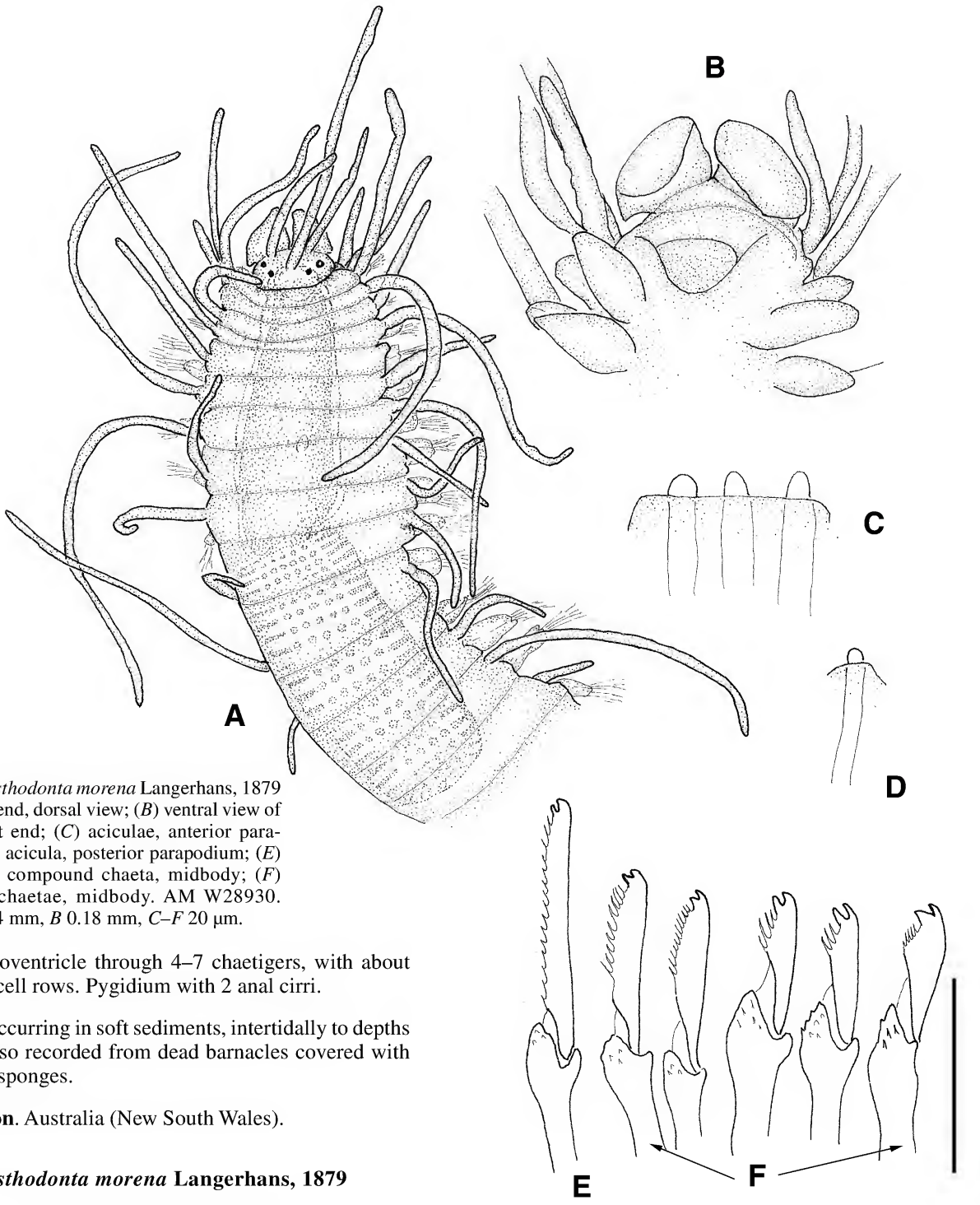


Fig. 40. *Opisthodonta morena* Langerhans, 1879 (*A*) anterior end, dorsal view; (*B*) ventral view of anteriormost end; (*C*) aciculae, anterior parapodium; (*D*) acicula, posterior parapodium; (*E*) long-bladed compound chaeta, midbody; (*F*) compound chaetae, midbody. AM W28930. Scales: *A* 0.4 mm, *B* 0.18 mm, *C–F* 20 µm.

38A,G). Proventricle through 4–7 chaetigers, with about 23 muscle cell rows. Pygidium with 2 anal cirri.

Habitat. Occurring in soft sediments, intertidally to depths of 50 m; also recorded from dead barnacles covered with encrusting sponges.

Distribution. Australia (New South Wales).

Opisthodonta morena Langerhans, 1879

Figs 40A–F, 41A–F, 42A,B

Opisthodonta morena Langerhans, 1879: 547, fig. 12.—Pérès, 1954: 107, figs 3–6.—Laubier, 1966: 249.—Storch, 1966: 173, pl.1, fig. 2.—Hartmann-Schröder, 1971: 100, Figs 1–3.—Campoy, 1982: 307.—San Martín, 2003: 54, figs 15, 16.

Material examined. TASMAN SEA: Reef flat near *Yoshin Maru Iwaki* wreck, Elizabeth Reef, 29°55.8'S 159°01.3'E, reef flat at low tide, 14 Dec 1987, 1 on SEM stub (AM W28874); Taupo Seamount, 33°16.85'S 156°09.15'E, limestone & sand bottom, 244 m, coll. J.K. Lowry & party, 2 May 1989, 2 on SEM stub (AM W28875); Taupo Seamount, 33°16.85'S 156°09.15'E, limestone & sand bottom, 244 m, coll. J.K. Lowry & party, 2 May 1989, 2 (AM W28930). WESTERN AUSTRALIA: Goss Passage, Beacon Is., 28°25.5'S 113°47'E, dead *Acropora* plates covered in algae, sponges & ascidians, 23 m, coll. P.A. Hutchings, 19 May 1994, 1 (AM W28384); N end of Long Is., 28°27.9'S 113°46.3'E, dead coral substrate covered in coralline & brown algae, 5.5 m, coll. C. Bryce, 22 May 1994, 1 (AM W28954). N end of Long Is., 28°28.3'S 113°46.3'E, dead coral substrate, coralline algae, boring bivalves, 8 m, coll. C. Bryce, 22 May 1994, 1 (AM W28955); Goss Passage, Beacon Is., 28°25.5'S 113°47'E, dead plates of *Acropora* coral covered in coralline algae, 8 m, coll. P.A. Hutchings, 22 May 1994, 1 (AM W28956); Goss Passage, Beacon Is., 28°25.5'S 113°47'E, dead plates of *Acropora* coral, 8 m, coll. P.A. Hutchings, 19 May 1994, 1 (AM W28957); Off jetty adjacent to Fisheries Hut, Beacon Is., 28°25.5'S 113°47'E, dead coral substrate, plate-like *Acropora* & *Montipora* spp., 12 m, coll. P.A. Hutchings, 23 May 1994, 1 (AM W28958); Reef S of Lucas Is., Brunswick Bay, Kimberley region, 15°16'S 124°29'E, 2 m, coll. P.A. Hutchings, 24 July 1988, several (AM W28931).

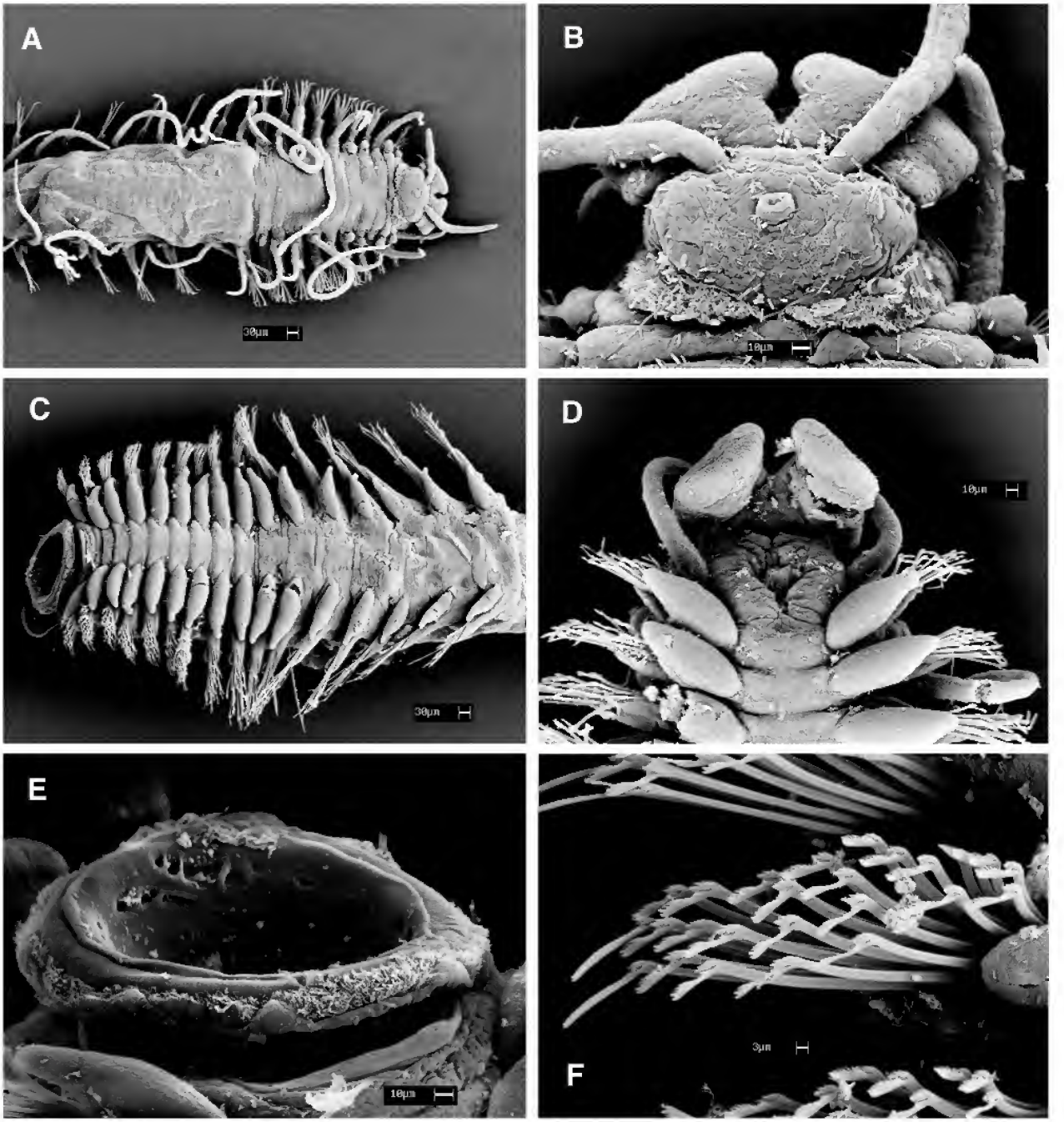


Fig. 41. SEM of *Opisthodonta morena* Langerhans, 1879 (*A*) anterior end, dorsal view; (*B*) detail of prostomium (median antenna missing); (*C*) anterior end, ventral view; (*D*) detail of anteriormost end, ventral view; (*E*) pharyngeal opening; (*F*) compound chaetae, anterior parapodium. AM W28874, AM W28875.

Description. Body fragile from proventricular segments, only anterior fragments examined, longest fragment 3.7 mm long, 0.4 mm wide, with 26 chaetigers. Prostomium oval to pentagonal (Figs 40A, 41B), with 2 pairs of eyes in trapezoidal arrangement and 2 anterior eyespots; median antenna inserted on middle of prostomium, more than three times combined length of prostomium and palps; lateral antennae about half length of median antenna, inserted near anterior margin of prostomium. Palps broad, large, trapezoidal, thin, usually ventrally folded (Figs 40B, 41D); apparently free from each other (Fig. 40A), but fused basally (Fig. 41B). Peristomium dorsally reduced, covered by chaetiger 1; dorsal tentacular cirri similar to median antenna, but shorter, ventral tentacular cirri about two thirds length of dorsal ones. Posterior margin of prostomium and nuchal organs densely ciliated (Figs 40A, 41B) dorsal cirri similar to antennae, smooth, filiform, long and slender, long on anterior segments, (Figs 40B, 41A), alternating long cirri, twice body width, and short cirri, shorter than body width, from proventricular segments onwards. Parapodial lobes conical, distally bifid (Fig. 40B). Ventral cirri large, ovate, partially fused to parapodial lobes on anterior segments (Figs 40C, 41D), conical, shorter and not fused from proventricular segments onwards (Fig. 41C). Compound chaetae numerous, 17–23 anteriorly, decreasing to about 7 on midbody, heterogomph, shafts subdistally spinose, similar throughout; on midbody, 2–3 compound chaetae with slender, elongate, bidentate blades (Figs 40E, 41F,

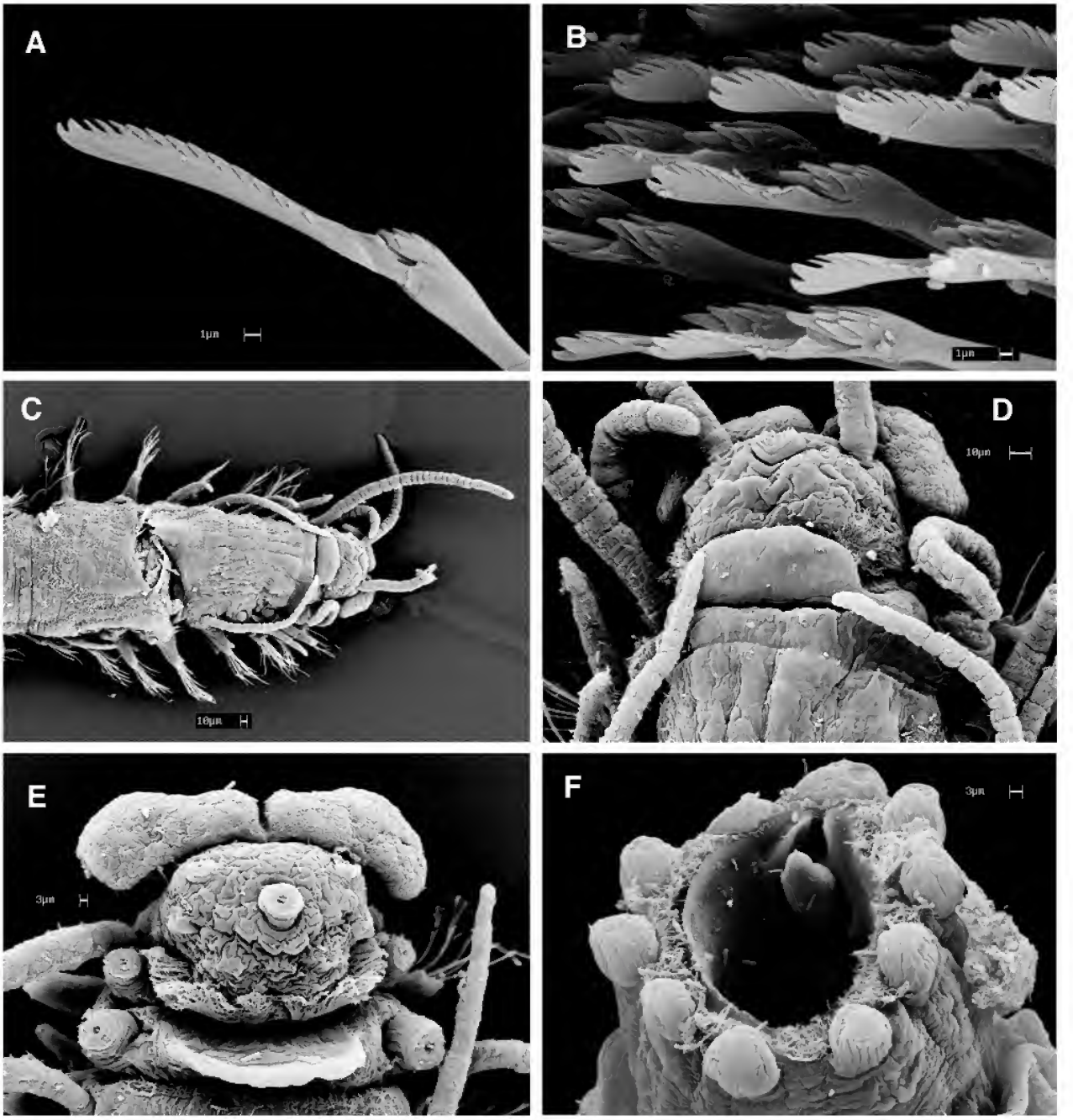


Fig. 42. SEM of *Opisthodonta morena* Langerhans, 1879 (*A*) long-bladed compound chaeta; (*B*) compound chaetae. SEM of *Pionosyllis yolandae* n.sp. (*C*) anterior end, dorsal view; (*D,E*) detail of prostomium and anteriormost segments; (*F*) pharyngeal opening. *A,B*: AM W28874, AM W28875; *C–F*: AM W28876.

42A), about 25–26 µm in length, short spines on margin, 2 compound chaetae with similar blades but shorter, 15–16 µm in length, marginal spines, distally directed, and remaining compound chaetae with short, bidentate blades, proximal tooth longer than distal tooth, and few spines on margin (Figs 40F, 41F, 42B), moderate in length, distally directed, dorsoventral gradation in length within fascicle, 13 µm in length dorsally, 8 µm in length ventrally. Dorsal and ventral simple chaetae absent. Anterior parapodia with 3 aciculae, straight, distally broad (Fig. 40C), diminishing to single acicula posteriorly (Fig. 40D). Pharynx long and wide, through 9–11 segments, pharyngeal tooth inserted posteriorly (Fig. 40A), on about chaetigers 7–8; pharyngeal opening with some soft papillae and dense layer of cilia (Fig. 42E). Proventricle through 6 segments, with about 24 muscle cell rows.

Remarks. This species has been reported widely from tropical and subtropical regions; we have examined material from the Mediterranean, and the European Atlantic coast and they appear morphologically similar. A molecular study would be useful to confirm whether this is a widely distributed species or a suite of sibling species.

Habitat. Occurring interstitially in coarse and coral sand, seagrasses, mud, from intertidal to depths greater than 240 m.

Distribution. Western Atlantic, Mediterranean, Red Sea, Australia (New South Wales, Western Australia).

Genus *Paraehlersia* San Martín, 2003

Paraehlersia San Martín, 2003: 61.

Type species. *Ehlersia ferrugina* Langerhans, 1881, designated by San Martín, 2003.

Diagnosis. Body long, stout, with numerous segments, adults 5 mm or greater in length, dorsally convex. Prostomium with 4 eyes and pair of anterior eyespots. Three antennae. Median antenna inserted on middle of prostomium. Palps basally fused, with dorsal furrow. Two pairs of tentacular cirri. Nuchal organs as 2 ciliated grooves between prostomium and peristomium. Antennae, tentacular cirri and anterior dorsal cirri of adults articulated to irregularly articulated depending upon size, remaining dorsal cirri smooth. Dorsal ciliary bands on segments. Parapodia without prechaetal lobes; digitiform, retractile papilla between parapodial lobes and dorsal cirri of some parapodia. Compound chaetae heterogomph, including one or more chaetae with spiniger-like blades and several bidentate falcigerous blades, anteriorly with both teeth similar, posteriorly with proximal tooth longer and more robust than distal tooth. Aciculae acuminate. Pharynx and proventricle of similar size. Pharyngeal tooth anteriorly located. Reproduction by epigamy (San Martín, 2003).

Key to Australian species of *Paraehlersia*

1 Falcigers and ventral simple chaetae provided with distal long spines on margin, reaching or extending beyond level of proximal tooth ..... *P. weissmannioides*

—— Chaetae with short spines on margin (Fig. 44D) ..... *P. ehlersiaeformis*

Paraehlersia ehlersiaeformis (Augener, 1913) n.comb.

Figs 43D–F, 44A–K, 45A–F, 46A–C

Pionosyllis ehlersiaeformis Augener, 1913: 225, figs 31, 32.

Syllis (Ehlersia) ferrugina.—Haswell, 1920: 101, pl. 12, figs 3–10. Not Langerhans, 1881: 104.

Typosyllis (Langerhansia) ferrugina.—Hartmann-Schröder, 1981: 30; 1987: 37; 1989: 23; 1991: 33. Not Langerhans, 1881: 104.

Material examined. AUSTRALIA: NEW SOUTH WALES: Taupo Seamount, Tasman Sea, 33°16.85'S 156°09.15'E, limestone & sand bottom, 244 m, coll. J.K. Lowry & party on RV *Franklin*, 2 May 1989, 1 on SEM stub (AM W28899); Taupo Seamount, Tasman Sea, 33°16.85'S 156°09.15'E, limestone & sand bottom, 244 m, coll. J.K. Lowry & party on RV *Franklin*, 2 May 1989, 22 (AM W28939); Pittwater, 33°35.78'S 151°18.33'E, sand, 13.8 m, coll. Australian Museum Party, 22 Apr 1994, 2 (AM W23925); Pittwater, 33°35.77'S 151°18.34'E, muddy sand, 14.9 m, coll. Australian Museum Party, 9 Oct 1995, 1 on SEM stub (AM W23926); Bass Point, 34°36'S 150°54'E, 50 m, The Ecology Lab for RMI/Pioneer Project, 1 Feb 1990, 1 (AM W23063); Halfway Reef, 200 m S of Sullivan Reef, Ulladulla, 35°21.42'S 150°29.31'E, airlift over sponges, Bryozoa & Hydrozoa, 15 m, coll. K. Attwood & party, 3 May 1997, 1 on SEM stub (AM W28221); N side of Bannister Head, north of Ulladulla, 35°19.15'S 150°29.12'E, grey sponge from top of boulder, 18 m, coll. K. Attwood, 6 May 1997, few (AM W28223); Murray's Beach, Jervis Bay, 35°07.5'S 150°46'E, 10 m, coll. P.A. Hutchings, 23 Jan 1973, 2 (AM W28413); 350 m S of southern entrance to Jervis Bay, 35°7.7'S 150°46.05'E, 23 m, coll. P.A. Hutchings, 22 July 1972, 1 (AM W28436); S of Worang Point, Calle Calle Bay, Twofold Bay, 37°3.6'S 149°56.5'E, 6.1 m, coll. S. Keable, P. Albertson, 21 Feb 1985, 1 (AM W28440). SOUTH AUSTRALIA: 7 km NW of Port Davis Creek, Port Pirie, Spencer Gulf, 33°16'S 137°51'E, subtidal, unvegetated, 9.3 m, coll. T.J. Ward & party, Mar 1980, 1 (AM W21772); Boston Bay, Port Lincoln 34°51'S 135°51'E, washings from sheltered weedy rock, 2 m, coll. I. Loch, 12 Feb 1985, 1 (AM W28937); Billy Lights Point, Port Lincoln, 34°45'S 135°53'E, stone washings from sheltered intertidal rocks, coll. I. Loch, 15 Feb 1985, 1 (AM W28938). WESTERN AUSTRALIA: Goss Passage, Beacon Is., 28°25.5'S 113°47'E, dead plates of *Acropora* coral, 8 m, coll. P.A. Hutchings, 19 May 1994, several (1 epigamic on SEM stub) (AM W28373); Goss Passage, Beacon Is., 28°25.5'S 113°47'E, dead plates of *Acropora* coral covered in coralline algae, 8 m, coll. P.A. Hutchings, 22 May 1994, several (AM W28375); NE entrance to Goss Passage, Beacon Is., 28°27.9'S 113°46.7'E, dead branching *Acropora*, coralline & brown algae, 24 m, coll. P.A. Hutchings, 25 May 1994, 4 (AM W28377); Off S end of Long Is., Beacon Is., 28°28.8'S 113°46.3'E, dead coral substrate covered in coralline algae, 4.5 m, coll. P.A. Hutchings, 25 May 1994, 1 (AM W28379); Goss Passage, Beacon Is., 28°25.5'S 113°47'E, dead branching coral covered in coralline algae, 10 m, coll. P.A. Hutchings, 18 May 1994, 1 (AM W28382); Goss Passage, Beacon Is., 28°25.5'S 113°47'E, dead *Acropora* plates covered in algae, sponges & ascidians, 32 m, coll. P.A. Hutchings, 19 May 1994, 1 (AM W28383); Goss Passage, Beacon Is., 28°25.5'S 113°47'E, dead *Acropora* plates covered in coralline algae, 20 m, coll. P.A. Hutchings, 20 May 1994, 1 (AM W28385); E side of West Wallabi Is., 28°27.9'S 113°40.9'E, in *Posidonia* root mat, plus epifauna, 1.5 m, coll. P.A. Hutchings, 26 May 1994, several (AM W28388); NE entrance to Goss Passage, Beacon Is., 28°27.9'S 113°46.7'E, under boulders in coral sand at foot of reef slope, 33 m, coll. P.A. Hutchings, 25 May 1994, 2 (AM W28389); Wallabi Group of Is., 28°34.65'S 113°46.46'E, diverse sponges & rubble, 49 m, coll. P.A. Hutchings on WA FRV *Flinders*, 28 Jun 1994, 1 (AM W28391); Wallabi Group of Is., 28°23.61'S 113°45.09'E, sponge & shell debris from scallop beds, 35 m, coll. P.A. Hutchings on WA FRV *Flinders*, 30 May 1994, 1 (AM W28394); Off S end of Long Is., Beacon Is., 28°28.8'S 113°46.3'E, dead coral substrate covered in coralline algae, 4.5 m, coll. P.A. Hutchings, 25 May 1994, 2 (AM W28934); N end of Long Is., 28°28.3'S 113°46.3'E, dead coral substrate, coralline algae, boring bivalves, 8 m, coll. C. Bryce, 22 May 1994, few (AM W28972); N end of Long Is., 28°27.9'S 113°46.3'E, dead coral substrate covered in coralline & brown algae, 5.5 m, coll. C. Bryce, 22 May 1994, several (AM W28973); Wallabi Group of Is., 28°27.05'S 113°45.10'E, medium to fine sand & shell debris from scallop beds, 36.5 m, coll. P.A. Hutchings on WA FRV *Flinders*, 30 May 1994, 1 (AM W28935); 5 km offshore, Bush Bay, 30 km S of Carnarvon, 25°10'S 113°39'E, shallow strap-leaved seagrass beds, 2 m, coll. J.K. Lowry & R.T. Springthorpe, 6 Jan 1984, 1 (AM W28371); N end of beach, Bundegi Reef, Exmouth Gulf, 21°49'S 114°11'E, rocky rubble, coralline algae with green epiphyte, 1.5 m, coll. H.E. Stoddart, 4 Jan 1984, 1 (AM W28936); Reef S of Lucas Is., Brunswick Bay, Kimberley region, 15°16'S 124°29'E, 2 m, coll. P.A. Hutchings, 24 July 1988, 1 (AM W28940); north end of beach, Bundegi Reef, Exmouth Gulf, 21°49'S 114°11'E, rocky rubble, coralline algae with green epiphyte, 1.5 m, coll. H.E. Stoddart, 4 Jan 1984, several (AM W28974). Syntype: ZMH (P-8786), Sharks Bay, Western Australia.

Description. Body without colour markings, some specimens broad anteriorly (Fig. 43D), others slender, filiform, about 9 mm long, 0.4 mm wide, with 75 chaetigers. Prostomium oval to circular, 4 eyes arranged in open trapezoidal pattern. Median antenna long, slender, with numerous articulations, usually 2–3 times longer than combined length of prostomium and palps, inserted on middle of prostomium; lateral antennae similar to median one, but shorter, inserted in front of anterior eyes. Palps slightly longer than prostomium, triangular (Figs 43E, 44A). Peristomium distinct, similar in length to subsequent segments; tentacular cirri similar to antennae, dorsal tentacular cirri slightly longer than lateral antennae, ventral ones about two thirds length of dorsal ones. Anterior dorsal cirri irregularly articulated (Figs 43E, 44A), becoming

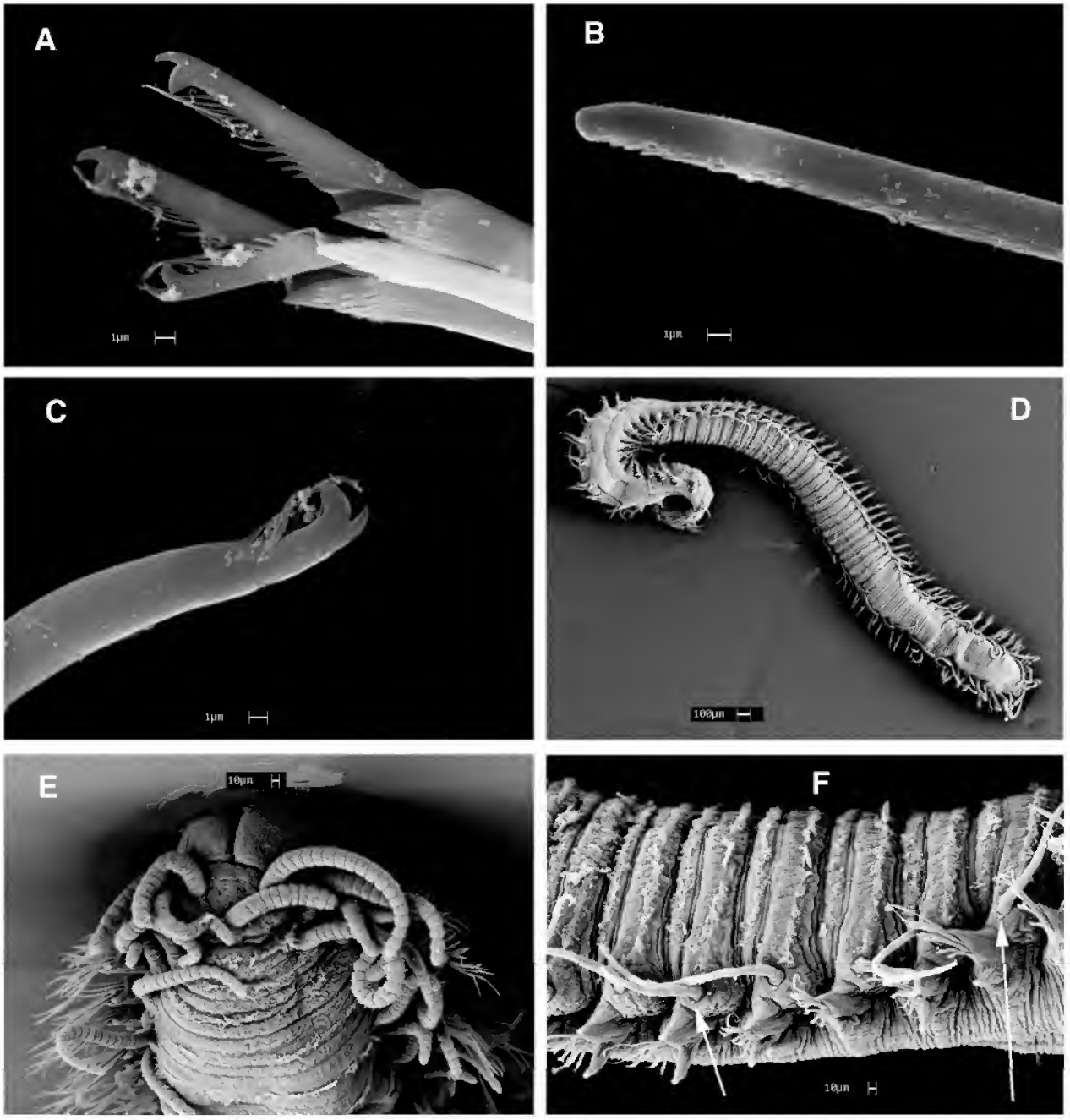


Fig. 43. SEM of *Paraehlersia weissmannioides* (Augener, 1913) (*A*) compound chaetae, posterior parapodium; (*B*) dorsal simple chaeta; (*C*) ventral simple chaeta. SEM of *Paraehlersia ehlersiaeformis* (Augener, 1913) (*D*) complete specimen, dorsal view; (*E*) anterior end, dorsal view; (*F*) lateral view, midbody (arrows showing subcirral papillae). *A–C*: AM W28224; *D–F*: AM W23926, W28221, W28899.

smooth, filiform (Figs 43F, 44A), from chaetiger 5–6, shorter than anterior ones, alternating irregularly long cirri, slightly longer than body width, and shorter ones about equal to body width. Dorsum of each segment with 2 rows of cilia (Figs 43F, 45B), except anteriormost, with only 1 row (Fig. 43E). Subcirral papilla small (Figs 43F, 44B, 45B arrows, 45C), difficult to see, present on anterior and midbody segments. Parapodial lobes sub-rectangular (Fig. 44B). Ventral cirri digitiform, similar in length to parapodial lobes. Anterior parapodia with up to 12 compound chaetae, 2–4 with elongated, slender, blades about 33 µm in length, bidentate with both teeth similar (Fig. 44C), and short spines on margin; remaining chaetae with shorter blades, bidentate, both teeth similar, and dorsoventral gradation in length within fascicle (Fig. 44D), 18 µm in length dorsally and 11 µm in length ventrally. Progressively along body, 1–2 blades of dorsalmost compound chaetae becoming more elongated, spiniger-like, indistinctly bidentate, with short spines on margin (Fig. 44F,I), 47 µm in length on midbody, 50 µm in length on posterior parapodia. Blades of falcigers with large proximal tooth and shorter distal tooth, short spines on margin (Figs 44G,J, 45D,F, 46A), 10–15 µm in length on midbody, 10–11 µm in length on posterior parapodia; about 6–7 falcigers on midbody parapodia and 4–5 posteriorly. Dorsal simple chaetae from mid-posterior segments, distally bifid, with short subdistal spines (Figs 44H, 46B). Ventral

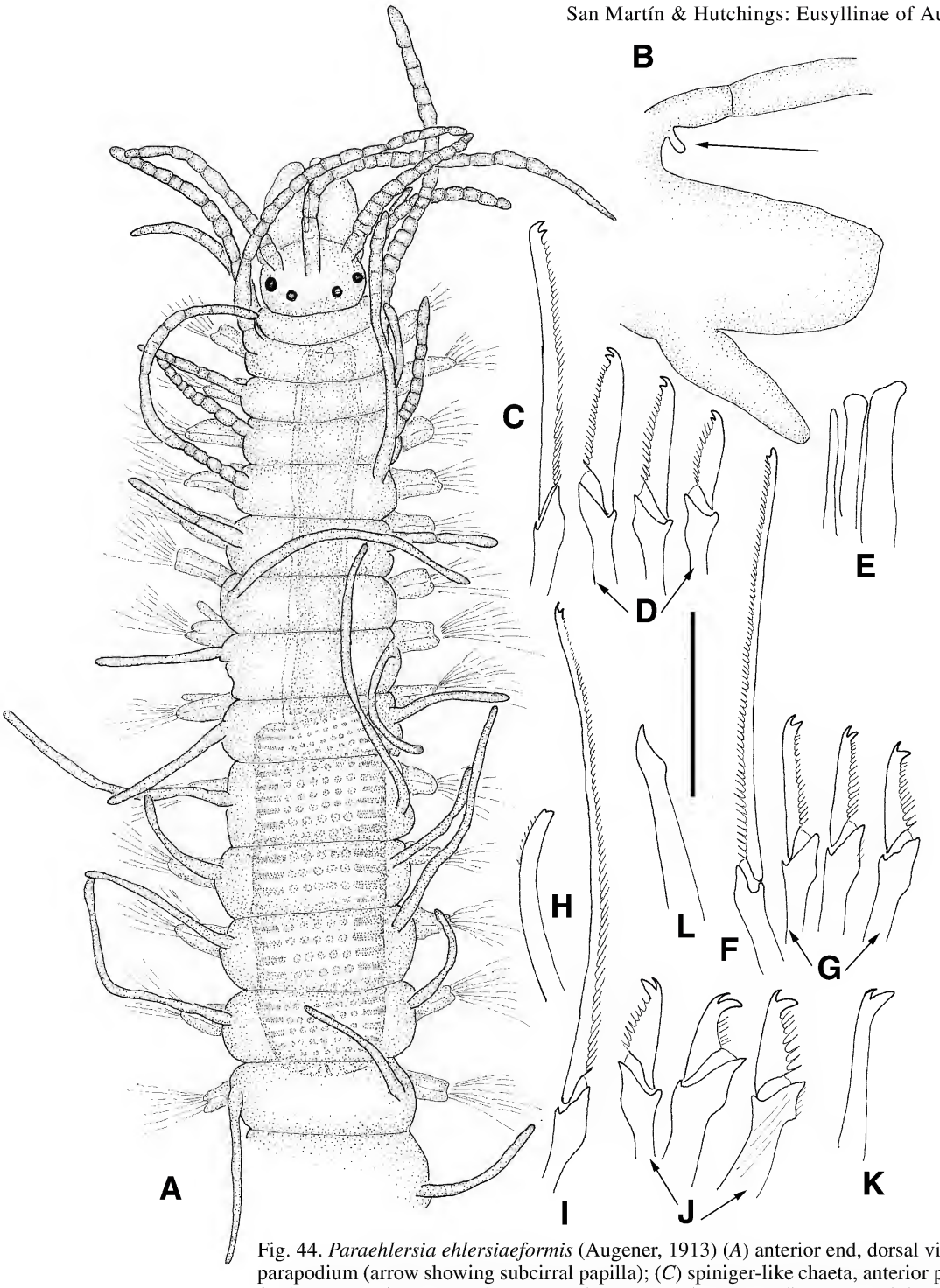


Fig. 44. *Paraehlersia ehlersiaeformis* (Augener, 1913) (*A*) anterior end, dorsal view; (*B*) anterior parapodium (arrow showing subcirral papilla); (*C*) spiniger-like chaeta, anterior parapodium; (*D*) falcigers, anterior parapodium; (*E*) aciculae, anterior parapodium; (*F*) spiniger-like compound chaeta, midbody; (*G*) falcigers, midbody; (*H*) dorsal simple chaeta; (*I*) spiniger-like compound chaeta, posterior parapodium; (*J*) falcigers, posterior parapodium; (*K*) ventral simple chaeta; (*L*) acicula, posterior parapodium. AM W28377. Scales: *A* 0.18 mm, *B* 48 µm, *C–L* 20 µm.

simple chaetae on posterior segments, smooth, strongly bidentate, proximal tooth long, robust, and distal tooth small (Figs 44K, 46C). Anterior parapodia with 3 aciculae (Fig. 63E), reducing to 1 from midbody, distally acuminate or lancet-shaped (Fig. 44L). Pharynx through 7 segments; pharyngeal tooth on anterior margin (Fig. 44A), surrounded by crown of 10 soft papillae and layer of cilia (Fig. 45A). Proventricle through 5 segments, with about 21 muscle cell rows. Pygidium with 2 long, filiform anal cirri and median papilla. Some specimens in epigamic reproductive phase, with long capillary chaetae on some parapodia (Fig. 45E).

Remarks. The specimens from Australia are similar to specimens of *P. ferrugina* Langerhans, 1879, which has been widely reported from Europe and northern Atlantic. Examination of one syntype of *P. ehlersiaeformis* (HZM P-8786) reveals that some blades of chaetae from posterior-most segments are slightly wider than those described from *P. ferrugina*. At this stage, we prefer to regard *P. ehlersiaeformis* and *P. ferrugina* as separate species. Augener (1913) reported *Syllis (Ehlersia) ferrugina* from Western Australia. This record, however, seems to be another species, probably belonging to the subfamily Syllinae.

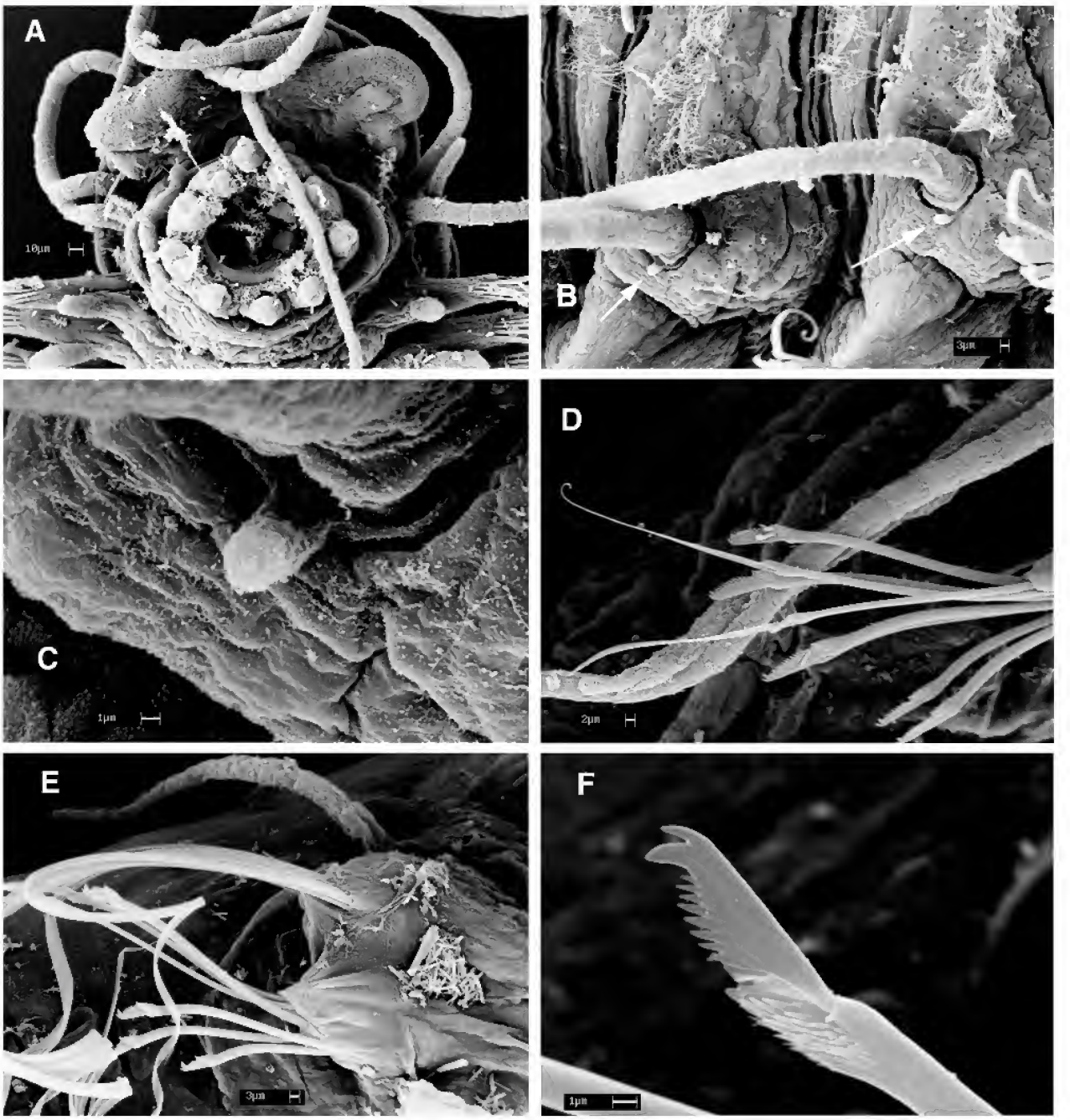


Fig. 45. SEM of *Paraehlersia ehlersiaeformis* (Augener, 1913) (*A*) everted pharynx; (*B*) subcirral papillae, showed by arrows; (*C*) detail of subcirral papilla; (*D*) compound chaetae, mid-anterior parapodium; (*E*) midbody parapodium of epigamic specimen, showing capillaries and notochaetae; (*F*) falciger, midbody. AM W23926, W28221, W28899.

Habitat. Reported from wide variety of substrates, especially abundant in algae and coralline concretions, from shallow waters to depths greater than 100 m.

Distribution. Australia (all States).

Paraehlersia weissmannioides (Augener, 1913) n.comb.

Figs 43A–C, 47A–I, 48A–F, 49D–F

Pionosyllis weissmannioides Augener, 1913: 223, fig. 30.
?*Ehlersia ferrugina* non Langerhans, Böggemann & Westheide, 2004: 418, fig. 6.

Material examined. AUSTRALIA: NEW SOUTH WALES: S ledge, Cook Is., 28°11.65'S 153°34.63'E, sand & shelly grit, 15 m, coll. K. Attwood, 9 Jun 1993,1 on SEM stub (AM W28224); E of North Head, Port Jackson, 33°48.77'S 151°20.98'E, sandy substratum, 60 m, coll. Australian Museum party, 12 Apr 1989, 1 (AM W20442). WESTERN AUSTRALIA: holotype (ZMH V-7949), Shark Bay, Useless Inlet, 26°08'S 113°21'E, 7 m depth.

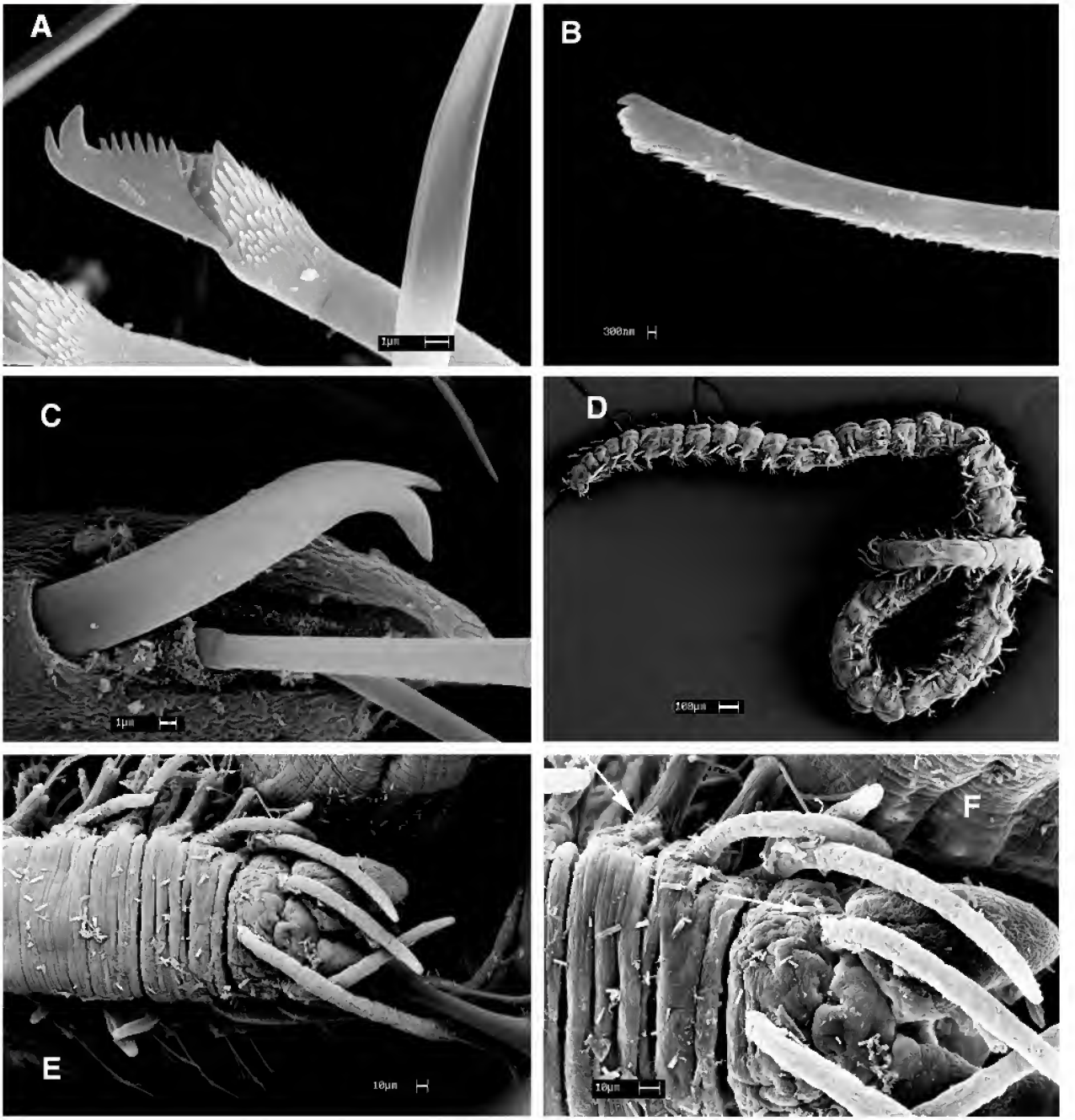


Fig. 46. SEM of *Paraehlersia ehlersiaeformis* (Augener, 1913) (*A*) falciger, posterior parapodium; (*B*) dorsal simple chaeta; (*C*) ventral simple chaeta. SEM of *Pionosyllis mariae* n.sp. (*D*) complete specimen; (*E*) anterior end, dorsal view; (*F*) detail of the same (arrows showing tufts of cilia). *A–C*: AM W23926, W28221, W28899; *D–F*: AM W28873.

Description. Body broad anteriorly (Fig. 49D), tapering posteriorly, yellowish, 7.2 mm long, 0.3 mm wide, with 61 chaetigers. Prostomium oval, nearly twice as wide as long; 4 eyes in open trapezoidal arrangement, and 2 anterior eyespots; median antenna longer than combined length of prostomium and palps, normally more than twice length, inserted near line between posterior eyes; lateral antennae about half of length of median antenna, inserted in front of anterior eyes (Fig. 49E), behind eyespots (Fig. 47A). Palps broad, slightly longer than prostomium, triangular. Peristomium distinct, similar in length to following segments; dorsal tentacular cirri longer than lateral antennae, shorter than median antenna; ventral tentacular cirri about two third length of dorsal tentacular cirri. Antennae, tentacular, and anterior dorsal cirri, elongated, articulated except basally (Figs 47A, 49E), with up to 20 articles; dorsal cirri becoming shorter and smoother; posterior to proventricle segments onwards, shorter than body width, totally smooth. Nuchal organs as 2 ciliated grooves between prostomium and peristomium (Fig. 49E,F). Dorsum of each segment provided with 2 ciliary bands and minute pores between bands (Fig. 47A,B). Subcirral papilla small, inconspicuous, but present on anterior and midbody segments (Figs 47B, 48B arrows, C). Parapodia conical, slightly elongate, distally bilobed (Fig. 49B). Ventral cirri digitiform, shorter than parapodial lobes. Most anterior

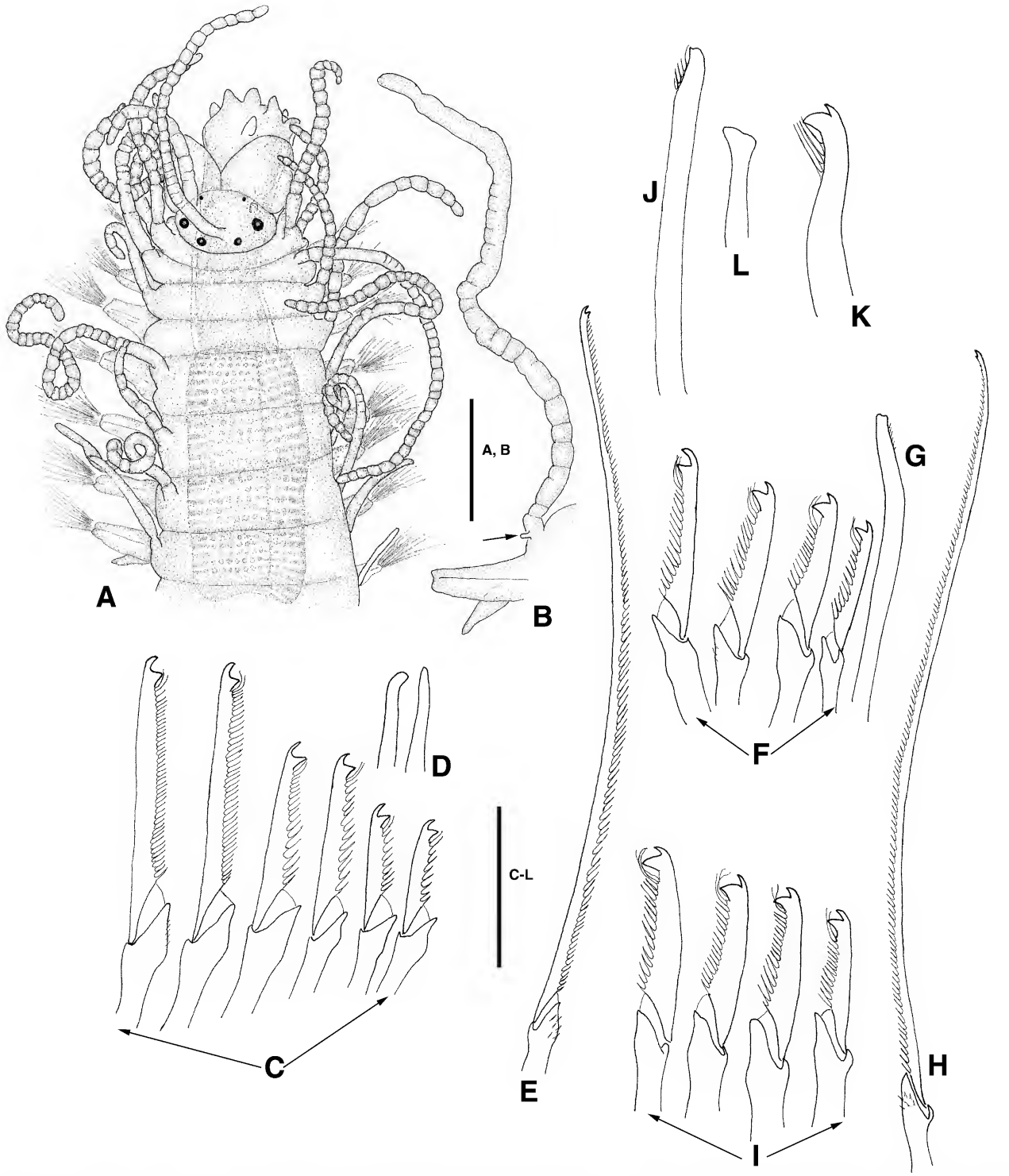


Fig. 47. *Paraehlersia weissmannioides* (Augener, 1913) (*A*) anterior end, dorsal view; (*B*) anterior parapodium, lateral view (arrow showing subcirral papilla); (*C*) compound chaetae, anterior parapodium; (*D*) aciculae, anterior parapodium; (*E*) spiniger-like compound chaeta, midbody; (*F*) falcigers, midbody; (*G*) dorsal simple chaeta, midbody; (*H*) spiniger-like compound chaeta, posterior parapodium; (*I*) falcigers, posterior parapodium; (*J*) dorsal simple chaeta, posterior parapodium; (*K*) ventral simple chaeta; (*L*) acicula, posterior parapodium. AM W20442. Scales: *A* 0.18 mm, *B* 97.5 μm, *C–L* 20 μm.

parapodia with about 15 compound chaetae, with strongly bidentate blades, both teeth well separated from each other, distal tooth slender, proximal robust, and long, fine spines on margin, 2–3 most distal ones longer than others, longer than proximal teeth (Figs 48C, 43D,E). Progressively posteriorly, most dorsal compound chaetae becoming longer and slender, spiniger-like, blades 95 μm in length on midbody, about 100 μm on posterior parapodia with fine, moderate spines on margin, spiniger like chaetae absent from last parapodia (Fig. 47E,H), indistinctly bidentate. Remaining compound chaetae similar to those of anterior segments (Figs 47F, 48F), progressively along body becoming larger, with stronger proximal tooth, slightly hooked (Figs 43A, 47I), reducing to 5. Dorsal simple chaetae

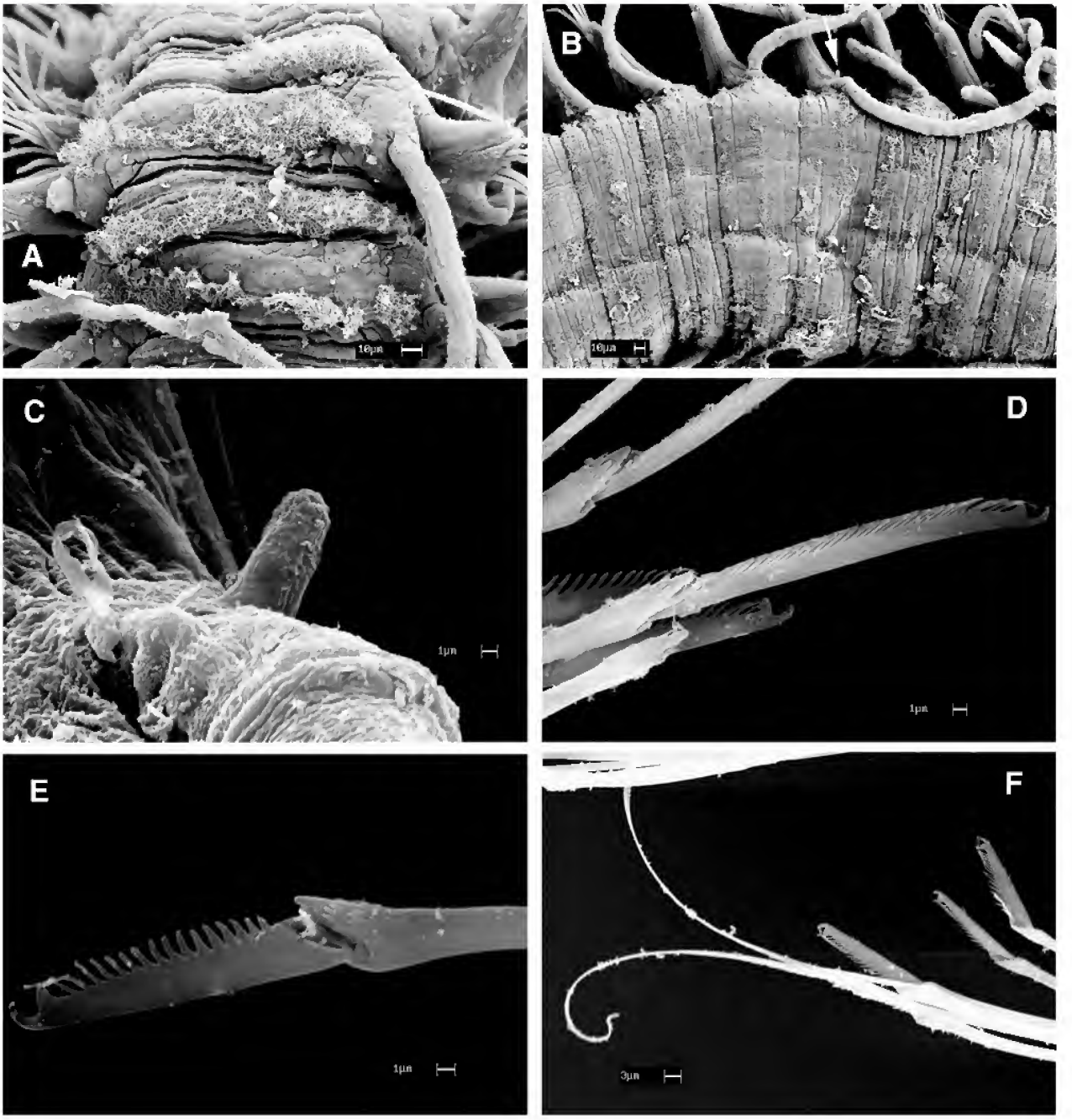


Fig. 48. SEM of *Paraehlersia weissmannioides* (Augener, 1913) (*A*) midbody segments, dorsal view; (*B*) same (arrow showing subcirral papilla); (*C*) subcirral papilla; (*D*) dorsal compound chaeta, anterior parapodium; (*E*) ventral compound chaeta, anterior parapodium; (*F*) compound chaetae, midbody. AM W28224.

from midbody, slender, distally slightly truncate and bifid, with short spines on margin (Figs 47G,J, 43B). Ventral simple chaetae on posterior parapodia, thick, strongly bidentate, with proximal tooth large, slightly hooked, and distal tooth much shorter than proximal one, with about 4 long spines on margin, reaching level of proximal tooth (Figs 47K, 43C). Anterior parapodia with 2–3 slender aciculae, one straight, others distally rounded (Fig. 47D); from proventricular segments onwards, acicula solitary, with oblique, short tip (Fig. 47L). Pygidium with 2 long anal cirri and median papilla. Pharynx everted on examined specimens, through about 7 segments; pharyngeal tooth anteriorly located, surrounded by crown of 10 soft papillae (Fig. 47A). Proventricle rectangular, through 4–5 segments, with about 22 muscle cell rows.

Remarks. The description of *Ehlersia ferrugina* by Böggemann & Westheide (2004) from specimens collected in coralline sand in Mahé (Seychelles) is similar to Australian specimens of *Paraehlersia weissmannioides* and they may represent the same species; but, the anterior compound chaetae seem to have both teeth less well separated, and the dorsal simple chaetae appear to be distally entire, not truncate and bifid, as occurs in the Australian material.

Habitat. Occurring in sand and shelly grit, in shallow depths, up to 15m.

Distribution. Australia (Western Australia, New South Wales); ?Seychelles.

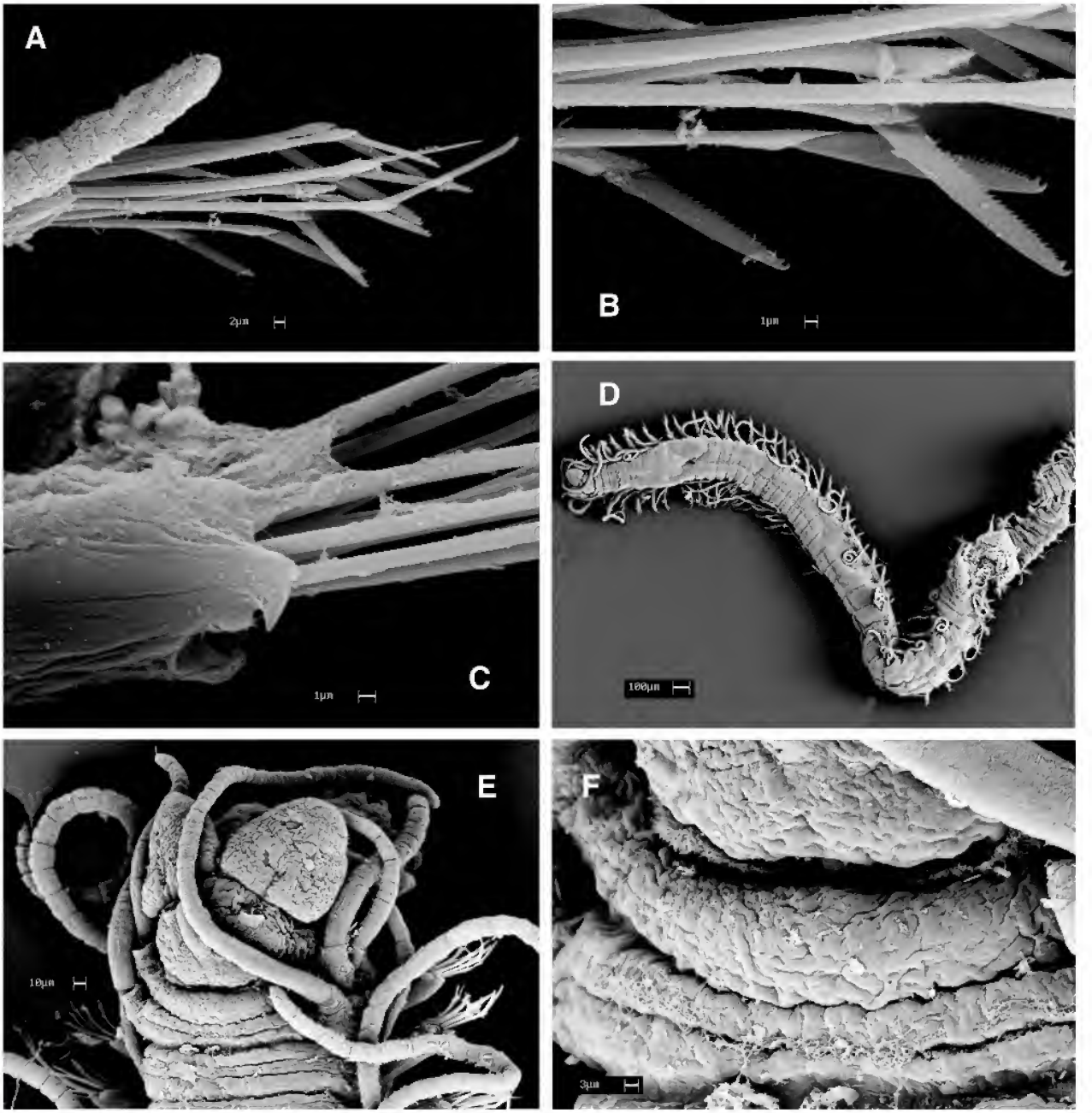


Fig. 49. SEM of *Pionosyllis yolandae* n.sp. (*A*) compound chaetae, anterior parapodium; (*B*) detail of the same; (*C*) parapodial lobe and acicula, midbody. SEM of *Paraehlersia weissmannioides* (Augener, 1913) (*D*) anterior part and midbody, dorsal view; (*E*) prostomium and anteriormost segments; (*F*) detail of nuchal organs. *A–C*: AM W28876, *D–F*: AM W28224.

Genus *Paraopisthosyllis* Hartmann-Schröder, 1991

Paraopisthosyllis Hartmann-Schröder, 1991: 27.

Type species. *Opisthosyllis brevicirra* Hartmann-Schröder, 1979, designated by Hartmann-Schröder, 1991.

Diagnosis. Body robust, cylindrical, broad anteriorly, tapered posteriorly, with many segments. Dorsal and ventral surfaces covered with numerous, small papillae. Prostomium with 4 lensed eyes and 3 antennae. Palps broad, fused at base, ventrally folded. Peristomium shorter than subsequent segments, sometimes covered dorsally by chaetiger 1; 2 pairs of tentacular cirri. Nuchal organs as 2 ciliated grooves between prostomium and peristomium. Dorsal and ventral cirri on all chaetigerous segments. Antennae, tentacular, anal and dorsal cirri smooth, enlarged, club-shaped to foliaceous. Dorsal cirri usually provided with distinct cirrophores; on some species, dorsal cirri of anterior segments alternating in size between large and small ones, larger cirri arising more dorsally. Parapodia with compound, heterogomph chaetae, and dorsal and ventral simple chaetae on posterior parapodia. Pharynx wide, with pharyngeal tooth inserted far from anterior rim. Proventricle wide, voluminous. Pygidium small, with 2 anal cirri.

Remarks. According to Hartmann-Schröder (1991), this genus belongs to the Eusyllinae. It has some unusual morphological characters, however, such as the shape and

arrangement of dorsal cirri, epidermal papillae, shape of pharynx and proventricle; its method of reproduction is unknown. It appears to be closely related to *Rhopalosyllis*, and therefore should be considered as a member of the subfamily Syllinae. Until its method of reproduction is determined, we are retaining it within the Eusyllinae according to its original designation. The genus is known only from Australia.

Key to Australian species of *Paraopisthosyllis*

1 Dorsal cirri inflated, club-shaped (Fig. 50A) 2
—— Dorsal cirri otherwise 3

2 Blades of some dorsal compound chaetae bidentate. Dorsal cirri alternating in size, larger ones located more dorsally than others ..... *P. alternocirra* n.sp.
—— All blades unidentate. Dorsal cirri all similar in size except those of chaetiger 1, inserted close to parapodial lobes (Fig. 53A) ..... *P. brevicirra*

3 Some dorsal cirri foliaceous (Fig. 55A). Pharyngeal tooth located on anterior half of pharynx ..... *P. phyllocirra*
—— Anterior dorsal cirri provided with distal, digitiform button (Fig. 54A). Pharyngeal tooth located on posterior half of pharynx ..... *P. ornaticirra* n.sp.

Paraopisthosyllis alternocirra n.sp.

Figs 50A–E, 51A–H, 52A–I

Opisthosyllis brevicirra.—Hartmann-Schröder, 1982: 57 (in part).

Material examined. HOLOTYPE (AM W26734) AUSTRALIA: WESTERN AUSTRALIA: Red Bluff, Kalbarri, 27°42'S 114°09'E, mixed coralline algae, 4 m, coll. J.K. Lowry, 10 Jan 1984. PARATYPES Red Bluff, Kalbarri, 27°42'S 114°09'E, round-leaved seagrass in shallow sand on rocky shore, 3.5 m, coll. R.T. Springthorpe, 10 Jan 1984, 3 (AM W28366); Rocky shore, Red Bluff, Kalbarri, 27°42'S 114°09'E, dictyotalean alga from cave, 4 m, coll. J.K. Lowry, 10 Jan 1984, 4 (AM W26784); Rocky shore, Red Bluff, Kalbarri, 27°42'S 114°09'E, brown algae from surf zone, 0.5 m, coll. H.E. Stoddart, 9 Jan 1984, 1 (AM W26783); Red Bluff, Kalbarri, 27°42'S 114°09'E, mixed coralline algae, 4 m, coll. J.K. Lowry, 10 Jan 1984, 7 + 1 on SEM stub (AM W28984); Inshore limestone reef, Ned's Camp, Cape Range National Park, 21°59'S 113°55'E, sponge covered with epiphytes, sediment & muddy worm tubes, 1.5 m, coll. R.T. Springthorpe, 2 Jan 1984, 1 (AM W28368).

Additional material examined. WESTERN AUSTRALIA: Rockingham, Point Peron, 32°17'S 115°44'E 115, algae, intertidal, coll. G. Hartmann-Schröder, 1 (HMZ P-17049); identified by Hartmann-Schröder as *Opisthosyllis brevicirra*.

Description. Complete specimen. Body anteriorly broad, tapered posteriorly (Fig. 52A), 6.7 mm long, 0.5 mm wide, with 59 chaetigers. Dark area of pigment dorsally on each segment, sometimes divided into 2 dorsal areas, anterior and posterior lateral areas; dark areas forming incomplete transverse row on posterior segments (Fig. 50A–C). Small, scattered papillae on lateral and ventral surfaces, more numerous on dorsum (Figs 50A,C, 52C,D). Prostomium oval, 4 small eyes arranged in open trapezoidal pattern, almost in straight line; lateral antennae inserted near anterior margin, oval, slightly rugose, shorter than combined length of prostomium and palps, median antenna similar to lateral but thicker, slightly longer, provided with dark inclusions, inserted slightly posteriorly to lateral ones, in front of eyes (Fig. 50A). Palps broad, longer than prostomium, ventrally folded (Figs 50D,E, 52C). Peristomium shorter than subsequent segments; tentacular cirri similar in shape to lateral antennae, but larger. Dorsal cirri of chaetiger 1 distally inflated, club-shaped, provided with dark inclusions, and located laterodorsally, anteriorly directed, partially covering prostomium (Fig. 50A,C,D); dorsal cirri of chaetigers 4 and 6 similar, but less inflated and more laterally inserted, subsequent dorsal cirri club-shaped, not as inflated as those of chaetigers 1, 4 and 6, without dark inclusions; alternating dorsal cirri laterodorsally located and others slightly smaller, more laterally located, cirri becoming smaller posteriorly (Fig. 50C,D). Dorsal cirri with cirrophores. Anterior parapodia with 7 compound, heterogomph chaetae, shafts with some spines on distal margin, and curved blades; 2 dorsalmost compound chaetae with relatively short, bidentate blades, with both teeth close to each other, and short spines on margin (Fig. 51C), 16 µm long; remaining compound chaetae with smooth, unidentate blades (Figs 51C, 52G), within fascicle slight dorsoventral gradation in length of blade, 22 µm in length dorsally, 17 µm in length ventrally. Progressively along body, chaetal blades becoming shorter and less bidentate; posterior parapodia with 6 compound chaetae, decreasing to 3 on posteriormost chaetigers, blades slightly hooked, smooth on margin, unidentate (Figs 51G, 52H), blades 15 µm in length dorsally, 10 µm in length ventrally. Dorsal simple chaetae slender, unidentate, smooth (Fig. 51F), present on posterior chaetigers (Fig. 52I). Ventral simple chaetae smooth, distally bent, unidentate, present on most posterior parapodia (Figs 51H, 52I). Anterior parapodia with 3–4 aciculae, distally rounded, single acicula on posterior parapodia (Fig. 51E). Pharynx wide, through 3–4 segments; pharyngeal tooth located about one third from anterior margin of pharynx (Fig. 51A). Margin of pharynx with 10 papillae (Figs 51A, 52E), each papilla with short cilia (Fig. 52F). Proventricle, longer than pharynx, extending through 3 segments, with 25–30 muscle cell rows. Pygidium small, with 2 anal cirri with dark inclusions, inflated and oval (Fig. 50B).

Remarks. This species is similar to *P. brevicirra* Hartmann-Schröder, 1979 (see below) but *P. alternocirra* has short and long dorsal cirri alternating along the anterior part of the body, distinct dark inclusions on the median antenna and large dorsal cirri, a colour pattern, and some dorsal compound chaetae on anterior and midbody parapodia with

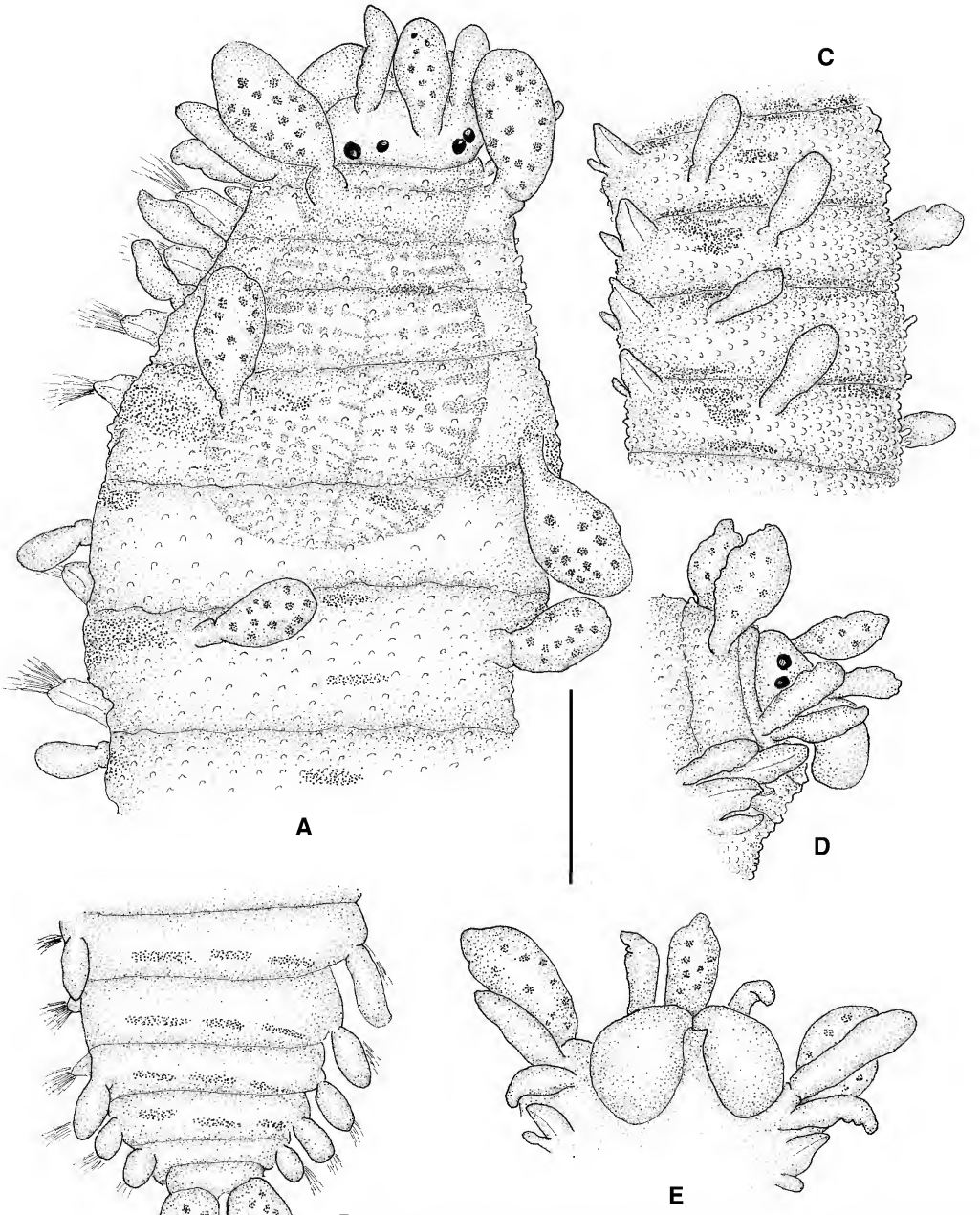


Fig. 50. *Paraopisthosyllis alternocirra* n.sp. (*A*) anterior end, dorsal view; (*B*) posterior end, dorsal view; (*C*) midbody, lateral view; (*D*) prostomium and anteriormost segments, lateral view; (*E*) same, ventral view. *A,B,E*: AM W26734; *C,D*: AM W26783. Scales: 0.18 mm

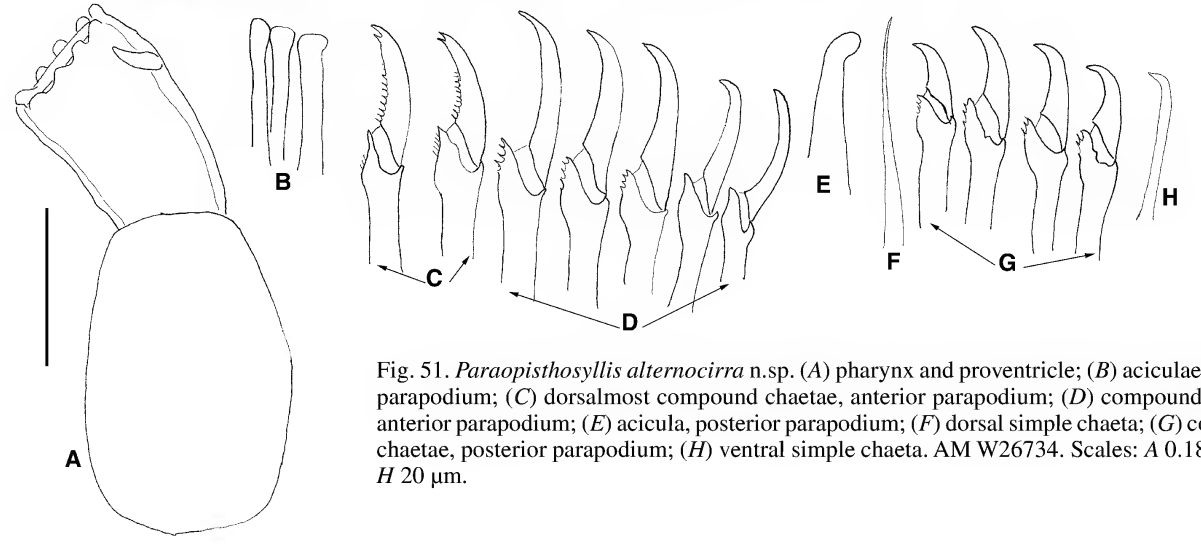


Fig. 51. *Paraopisthosyllis alternocirra* n.sp. (*A*) pharynx and proventricle; (*B*) aciculae, anterior parapodium; (*C*) dorsalmost compound chaetae, anterior parapodium; (*D*) compound chaetae, anterior parapodium; (*E*) acicula, posterior parapodium; (*F*) dorsal simple chaeta; (*G*) compound chaetae, posterior parapodium; (*H*) ventral simple chaeta. AM W26734. Scales: *A* 0.18 mm, *B–H* 20 μm.

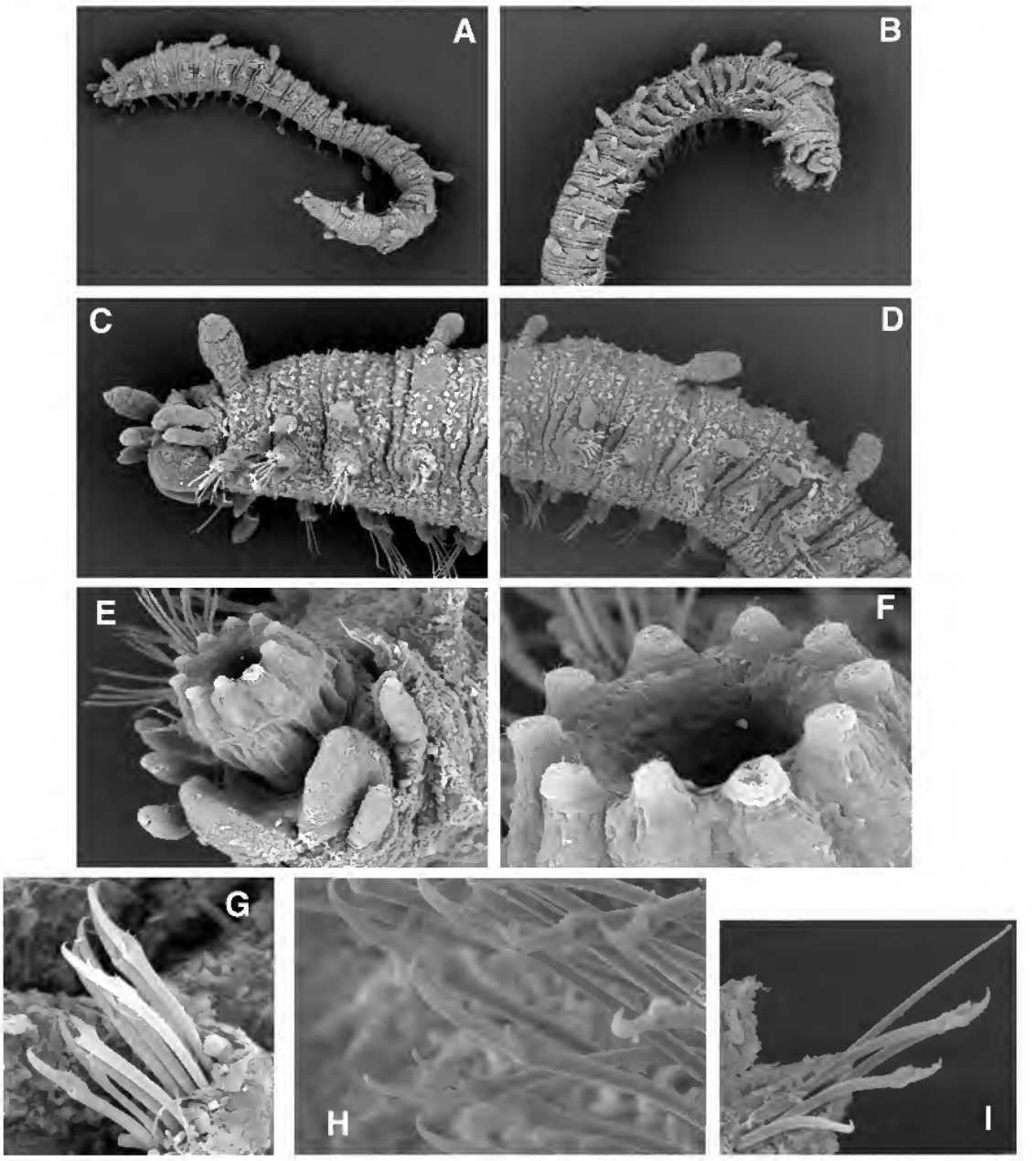


Fig. 52. SEM of *Paraopisthosyllis alternocirra* n.sp. (*A*) complete specimen, lateral view; (*B*) anterior end, lateral view; (*C*) prostomium and anterior segments, lateral view; (*D*) midbody, lateral view; (*E*) everted pharynx; (*F*) detail of pharyngeal papillae; (*G*) fascicle of chaetae, anterior parapodium; (*H*) midbody fascicle of chaetae; (*I*) posterior fascicle of chaetae. AM W28984.

bidentate blades. In contrast, *P. brevicirra* has only unidentate chaetae, dorsal cirri not as inflated and lacks dark inclusions on the antennae and cirri, and is colourless. The specimen reported as *Opisthosyllis brevicirra* by Hartmann-Schröder (1982) belongs to this new species and differs from the holotype of the taxon.

Habitat. Occurring in algae, seagrasses, and sponges; from intertidal to shallow depths.

Distribution. Australia (Western Australia).

Etymology. The specific name refers to the alternating sizes of the dorsal cirri along the body.

Paraopisthosyllis brevicirra (Hartmann-Schröder, 1979)

Fig. 53A–C

Opisthosyllis brevicirra Hartmann-Schröder, 1979: 57, figs 43–45. Not *Opisthosyllis brevicirra* Hartmann-Schröder, 1982: 57.

Material examined. AUSTRALIA: WESTERN AUSTRALIA: holotype (HZM P-15499), Port Hedland, close to Highway Motel, 19°38'S 119°31'E, filamentous algae with sand & debris, intertidal, 27 Sept. 1975, coll. G. Hartmann-Schröder.

Description. Incomplete specimen, 4.5 mm long, 0.5 mm wide, with 28 chaetigers, without pigment pattern (Fig. 53A). Numerous, scattered, rounded papillae covering

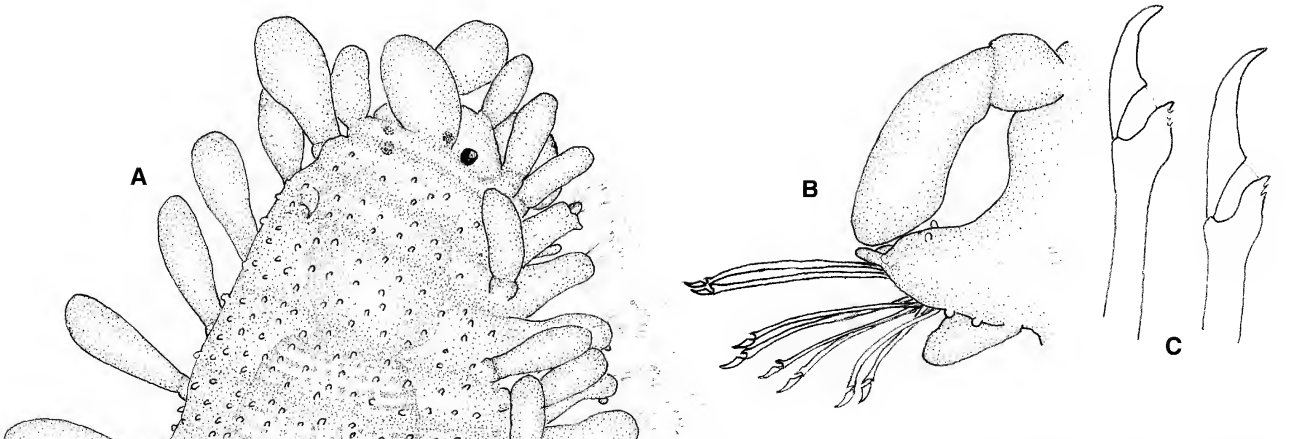


Fig. 53. *Paraopisthosyllis brevicirra* (Hartmann-Schröder, 1979) (*A*) anterior end, dorsal view; (*B*) midbody parapodium; (*C*) compound chaetae. HZM P-15499. Not scaled. Modified from Hartmann-Schröder, 1979.

dorsal and ventral surfaces, extending onto parapodia. Prostomium oval, 4 eyes arranged in open trapezoidal pattern; lateral antennae inserted near anterior margin, oval, shorter than combined length of prostomium and palps, median antenna similar to lateral but distinctly thicker, slightly longer, inserted posteriorly to lateral ones (Fig. 53A). Palps broad, longer than prostomium, ventrally folded (Fig. 53A). Peristomium shorter than subsequent segments; tentacular cirri similar in shape to lateral antennae, but longer. Dorsal cirri of chaetiger 1 distally inflated, club-shaped, laterodorsally located (Fig. 53A). Remaining dorsal cirri smaller, club-shaped, slightly elongate, not as inflated as those of chaetiger 1, inserted more laterally (Fig. 53A,B). Dorsal cirri with distinct cirrophores (Fig. 53B). Parapodia conical, with 2 distal papillae (Fig. 53B). Anterior parapodia with 8–9 compound, heterogomph chaetae, shafts with some spines on distal margin, and curved, unidentate blades, slightly shorter dorsally than ventrally, smooth on margin (Fig. 53C). Dorsal and ventral simple chaetae not seen. Anterior parapodia each with 3–4 aciculae, distally rounded, reducing to single acicula on posterior parapodia. Pharynx wide, extending through 3 segments; pharyngeal tooth located about one third from anterior margin of pharynx (Fig. 53A). Proventricle large, longer than pharynx, through 3 segments, with 25–26 muscle cell rows.

Remarks. One specimen 1 (HMZ P-17049) identified by Hartmann-Schröder as *Opisthosyllis brevicirra* belongs to *P. alternocirra* n.sp.

Habitat. Occurring in sand and debris, intertidally.

Distribution. Australia (Western Australia).

Paraopisthosyllis ornaticirra n.sp.

Fig. 54A–K

Material examined. HOLOTYPE (AM W28949) AUSTRALIA: WESTERN AUSTRALIA: Inshore limestone reef, Ned's Camp, Cape Range National Park, 21°59'S 113°55'E, *Caulerpa* sp., 1 m, coll. J.K. Lowry, 2 Jan 1984.

Description. Complete specimen. Body broad and robust anteriorly, tapered posteriorly, 7.8 mm long, 0.6 mm wide, with 63 chaetigers. Segmented pigmentation absent, but median antenna and anterior dorsal cirri each with 2 dark transverse areas, large dorsal cirri with more extensive pigmented area, anal cirri with single transverse band of pigment (Fig. 54A,C,D). Dorsal and ventral surfaces densely covered with small, rounded papillae (Fig. 54A). Prostomium rectangular, with 2 pairs of eyes arranged almost in line. Lateral antennae inserted in front of eyes, relatively short and slender; median antenna longer and thicker than lateral antennae, arising between eyes (Fig. 54A). Palps broad, as wide as prostomium, ventrally folded (Fig. 54A,B). Peristomium dorsally reduced, covered by chaetiger 1; dorsal tentacular cirri similar in shape to median antenna slightly longer and thicker, ventral tentacular cirri similar but smaller than dorsal ones. Dorsal cirri of chaetigers 1, 4, and 6 distinctly longer and larger than remaining dorsal cirri, inflated, except for chaetiger 6, with digitiform, non-pigmented terminal lobe, arising dorsolaterally (Fig. 54A). Remaining dorsal cirri with cirrophores; cirrostyles tapered, fusiform, shorter than half of body width, with 1–2 bands of dark pigment, midbody dorsal cirri lacking such pigment (Fig. 54D); posterior dorsal cirri oval, shorter than those of anterior chaetigers. Parapodia with anterior and posterior lobes (Fig. 54D). Compound chaetae with thick shafts, distally provided with strong serration, and short, strongly bidentate blades, with short, few spines on margin; anterior parapodia with about 15 compound chaetae, blades slender (Fig. 54F), about 13 µm in length. Compound chaetae becoming progressively thicker posteriorly, with blades bidentate; about 10–14 compound chaetae on midbody parapodia, blades 10–12 µm in length, terminal teeth increasing in size ventrally within fascicle (Fig. 54G). Number of compound chaetae per parapodium decreasing posteriorly, with only 3 on most posterior parapodia, similar to those of midbody (Fig. 54I). Dorsal simple chaetae on posterior parapodia, distally serrated and bifid (Fig. 54J). Ventral simple chaetae on most posterior parapodia, thick, strongly bidentate, smooth on margin (Fig. 54K). Anterior parapodia with 3 aciculae,

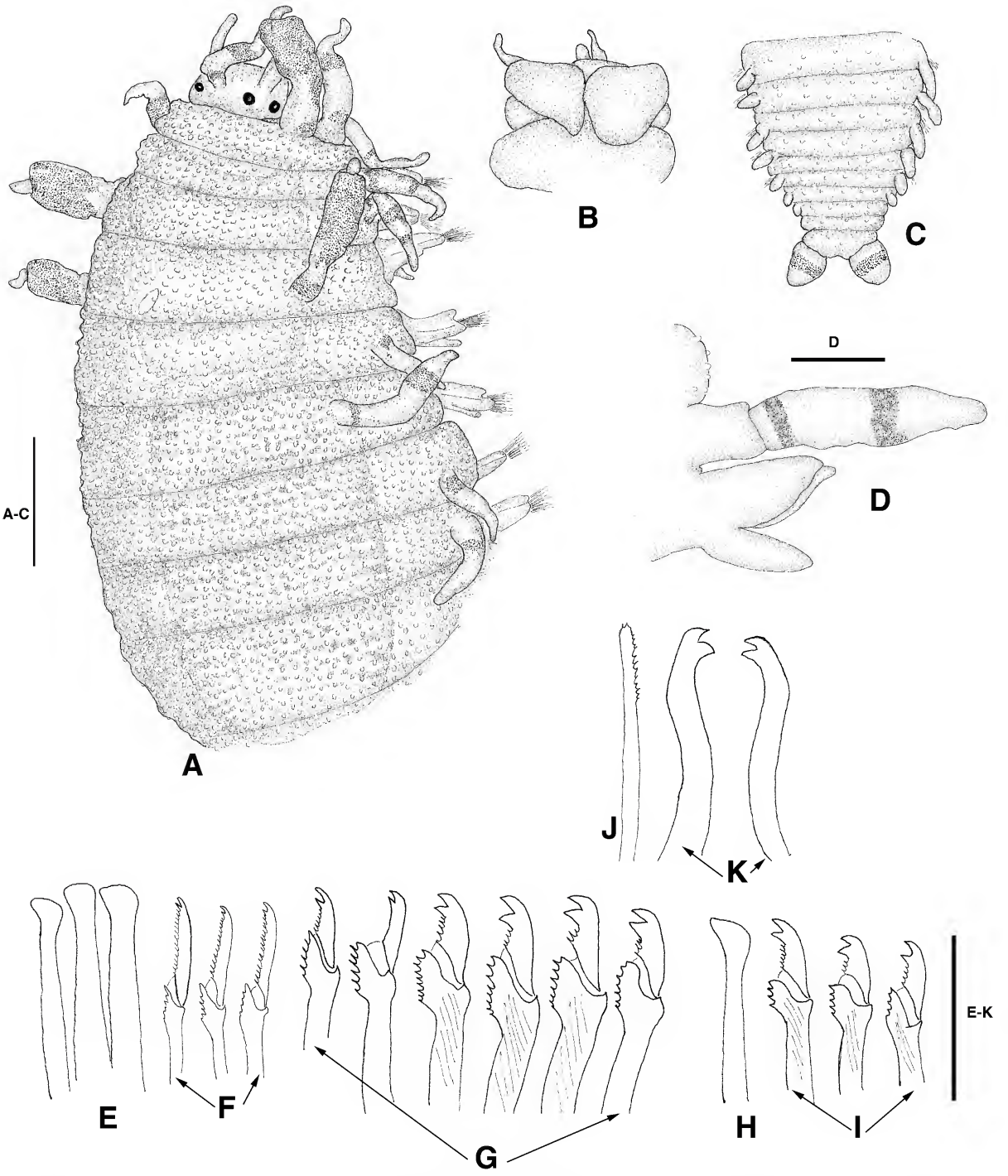


Fig. 54. *Paraopisthosyllis ornaticirra* n.sp. (*A*) anterior end, dorsal view; (*B*) prostomium and palps, ventral view; (*C*) posterior end, dorsal view; (*D*) midbody parapodium; (*E*) anterior aciculae; (*F*) compound chaetae, anterior parapodium; (*G*) compound chaetae, midbody; (*H*) acicula, posterior parapodium; (*I*) compound chaetae, posterior parapodium; (*J*) dorsal simple chaeta; (*K*) ventral simple chaetae. AM W28949. Scales: *A–C*: 0.18 mm, *D*: 92 μm, *E–K*: 20 μm.

distally rounded (Fig. 54E), posteriorly single acicula present, slightly bent at tip (Fig. 54H). Pharynx wide, through 3–4 segments; pharyngeal tooth located posteriorly. Proventricle similar in size to pharynx, with 30–35 muscle cell rows. Pygidium trapezoidal; anal cirri larger than posterior dorsal cirri, oval to egg-shaped.

Remarks. This species is easily distinguished from the other members of this genus by the shape of the enlarged dorsal cirri of chaetigers 1, 4, and 6, the pigment pattern present on the dorsal cirri and median antenna, and the presence of compound chaetae with strongly bidentate blades.

Habitat. Occurring in *Caulerpa*, in shallow depths.

Distribution. Australia (Western Australia).

Etymology. The species is named after the characteristic pigmentation pattern of the dorsal cirri.

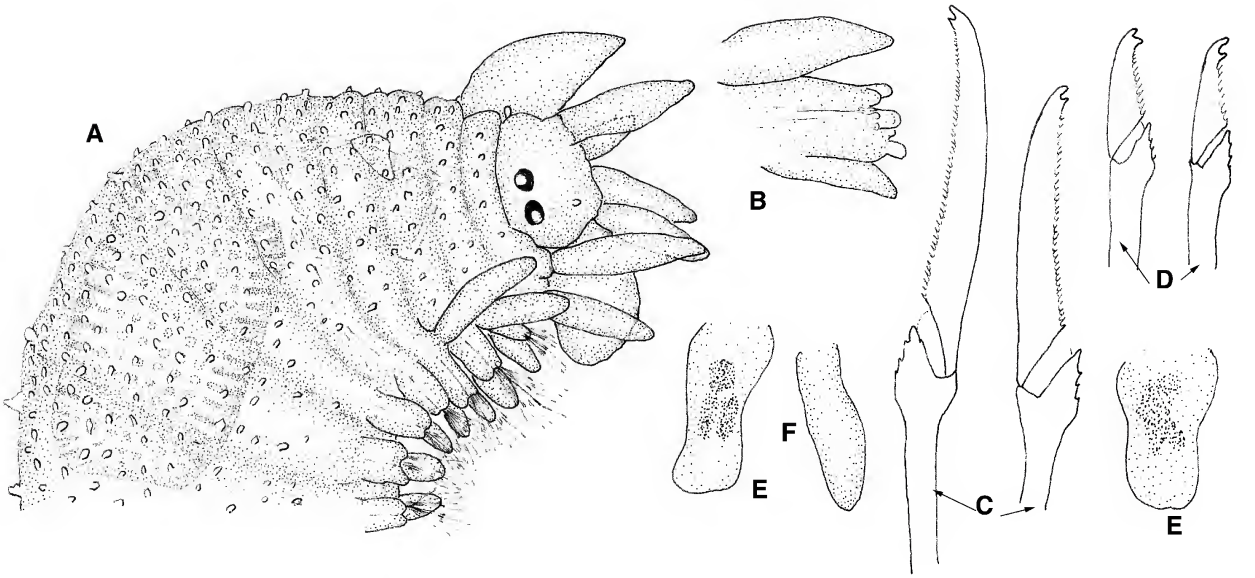


Fig. 55. *Paraopisthosyllis phyllocirra* Hartmann-Schröder, 1991 (*A*) anterior end, dorsolateral view; (*B*) anterior parapodium; (*C*) long and short compound chaetae, anterior parapodium; (*D*) same, posterior parapodium; (*E*) modified dorsal cirrus, posterior parapodia; (*F*) non-modified dorsal cirrus, posterior parapodium. HZM P-20533. Not scaled. Modified from Hartmann-Schröder, 1991.

Paraopisthosyllis phyllocirra Hartmann-Schröder, 1991

Fig. 55A–F

Paraopisthosyllis phyllocirra Hartmann-Schröder, 1991: 27, figs 26–29.

Material examined. HOLOTYPE (HZM P-20533), AUSTRALIA: QUEENSLAND: Heron Is., Great Barrier Reef, 23°27'S 151°55'E, coralline sand, intertidal, coll. G. Hartmann-Schröder.

Description. Incomplete specimen, 3.5 mm long, with 32 chaetigers, with some indistinct red-brownish spots dorsally and laterally. Numerous, scattered, rounded papillae covering dorsal (Fig. 55A) and ventral surfaces. Prostomium oval, 4 eyes arranged in open trapezoidal pattern; lateral antennae inserted near anterior margin, oval, shorter than combined length of prostomium and palps together, median antenna similar to lateral, originating slightly posterior to lateral antennae (Fig. 55A). Palps broad, longer than prostomium, ventrally folded (Fig. 55A). Peristomium slightly shorter than subsequent segments; tentacular cirri similar in shape to lateral antennae, but larger. Dorsal cirri of chaetiger 1 inflated, leaf-shaped, laterodorsally located (Fig. 55A), right one missing. Following dorsal cirri smaller, oval, not as inflated as those of chaetiger 1, arising more laterally (Fig. 55A,B); some dorsal cirri of posterior segments flattened, truncated, with some dark pigment (Fig. 55E), alternating with non modified dorsal cirri (Fig. 55F). Parapodia sub-rectangular, with 4–5 distal papillae (Fig. 55B). Anterior parapodia with 7–9 compound, heterogomph chaetae, shafts with some spines on distal margin, and curved, bidentate blades, within fascicle dorsoventral gradation in length of blades (Fig. 55C), with short spines on margin. Posterior compound chaetae similar to anterior ones, but with shorter blades and without any dorsoventral gradation in length within fascicle (Fig. 55D). Dorsal and ventral simple chaetae absent. Anterior parapodia with 3 aciculae, distally rounded, single acicula on posterior parapodia. Pharynx wide, through 3–4 segments; pharyngeal tooth occurs about third from anterior margin of pharynx (Fig. 55A). Proventricle large, longer than pharynx, through 3 segments, with 25 muscle cell rows.

Remarks. Shape of posterior dorsal cirri were not described in the original description.

Habitat. Occurring in coralline sand, intertidally.

Distribution. Australia (Queensland).

Genus *Pionosyllis* Malmgren, 1867

Pionosyllis Malmgren, 1867: 40.

Type species. *Pionosyllis compacta* Malmgren, 1867 by monotypy.

Diagnosis. Body ranges from meiofaunal to macrofaunal size (<5 to >10 mm in length), dorsally convex. Prostomium with 4 eyes, sometimes also pair of eyespots, sometimes without eyes. Three antennae. Prostomium sometimes with cheeks or lobes on large specimens. Median antenna inserted on middle of prostomium or anteriorly. Palps fused at bases, with dorsal furrow, or free from each other. Two pairs of tentacular cirri. Nuchal organs as 2 ciliated grooves between prostomium and peristomium. Antennae, tentacular cirri and dorsal cirri smooth, sometimes rugose, long, filiform, all similar; weakly articulated on some species. Ventral cirri not fused to parapodial lobes, those of anterior parapodia somewhat inflated on some species, inserted basally or distally on parapodial lobes. Heterogomph compound chaetae with bidentate falcigerous blades, teeth similar in size; some dorsal anterior and midbody falcigers slightly longer than others, decreasing in size in dorsoventral gradation within fascicle; some species with hemigomph or homogomph articulations and blades of compound chaetae different to those described above. Dorsal and ventral simple chaetae on some posterior parapodia, bidentate, with both teeth similar, sometimes absent. Parapodia

with or without prechaetal lobes. Pharynx and proventricle similar in size. Pharyngeal tooth anteriorly located, some species with tooth on middle of pharynx. Reproduction by epigamy. Pygidium small, with 2 smooth anal cirri.

Remarks. *Pionosyllis* as above defined is a heterogeneous, probably a polyphyletic group in need of revision. Currently, GSM and other authors are preparing a major revision of the group.

Key to Australian species of *Pionosyllis*

1 Blades of compound chaetae with tendon connecting proximal tooth with margin (Fig. 74D). Pharyngeal tooth located near anterior rim, on middle of pharynx or posteriorly in mid line 2

—— Blades of compound chaetae without such tendon 3

2 Pharyngeal tooth located just in front of middle of pharynx. Compound chaetae including short, strongly bidentate falcigers (Fig. 74C,D) ..... *P. rousei* n.sp.

—— Pharyngeal tooth located close to anterior margin of pharynx. Compound chaetae all elongated, with proximal tooth distinctly larger than distal tooth ..... *Pionosyllis* sp.

3 Pharyngeal tooth located far from anterior rim (Fig. 65A). Some dorsal cirri inflated 4

—— Pharyngeal tooth located on anterior rim or close to (Fig. 56A) 5

4 Body dark. Inflated dorsal cirri with distal button (Fig. 60D). Dorsoventral gradation in length of blades of compound chaetae ..... *P. fusigera*

—— Body with small red spots. Inflated dorsal cirri without distal button (Fig. 65B). Inverse dorsoventral gradation in length of blades of compound chaetae ..... *P. kalimna*

5 Ventral cirri inserted medially or distally on parapodial lobes. Dorsal cirri of 2 lengths, long and filiform and extremely short, exogonid-like dorsal cirri that alternate along body (Fig. 59A) ..... *P. corallicola*

—— Ventral cirri inserted at bases of parapodia. Dorsal cirri similar throughout or else differences between short and long cirri not so pronounced (Fig. 78A) 6

6 Segments posterior to proventricle fused in units of 2–3 segments. Palps completely free ..... *P. yolandae* n.sp.

—— Segments not fused. Palps fused at bases 7

7 Dorsal cirri (except some anteriormost) exogonid-like, short, slightly longer than parapodial lobes 8

—— Dorsal cirri long 10

8 Dorsal cirri more or less truncate, with some internal glands (Fig. 70C) ..... *P. mariae* n.sp.

—— Dorsal cirri otherwise, without internal glands (Fig. 56D) 9

9 Compound chaetae including spiniger-like, with elongated blades. Dorsal simple chaetae truncate (Fig. 56I) ..... *P. ancori* n.sp.

—— Compound chaetae only falcigers. Dorsal simple chaetae pointed, unidentate (Fig. 73G) ..... *P. mayteae* n.sp.

10 Distinct prechaetal lobe present. Acicula straight, extending beyond parapodial lobes (Fig. 67L). Blades of compound chaetae without long, fine spines; without spiniger-like chaetae. Large size, (>10 mm in length) ..... *P. kerguelensis*

—— Prechaetal lobe absent. Acicula distally knobbed, with 2 unequal lobes. Blades of compound chaetae with long, fine, distally ornamented spines; sometimes with spiniger-like chaetae. 5–10 mm in length 11

11 Without long, spiniger-like compound chaetae 12
—— With long, thin, spiniger-like compound chaetae (Fig. 63D) 13

12 Anteriormost parapodia distinctly enlarged, with compound chaetae provided with large, thick shafts, and short blades (Fig. 75B) ..... *P. serrata*
—— Parapodia and compound chaetae similar throughout ..... *P. koolalya* n.sp.

13 Anterior parapodia without elongated, spiniger like compound chaetae ..... *P. heterochaetosa* n.sp.
—— Spiniger-like chaetae from anterior chaetigers 14

14 Compound chaetae of anterior segments with coarse serration and distal tooth more or less broad, rounded. Falcigers without double curvature ..... *P. augeneri*
—— Compound chaetae similar throughout. Some falcigers provided with double curvature (Fig. 61C) ..... *P. hartmannschroederae* n.comb.

Pionosyllis ancori n.sp.

Fig. 56A–M

Material examined. HOLOTYPE (AM W29244). AUSTRALIA: QUEENSLAND: Outer Yonge Reef, Great Barrier Reef, 14°36'S 145°38'E, rock covered with pink coralline algae, encrusting sponges, 9 m, coll. P.A. Hutchings, 21 Jan 1977. PARATYPES 4 (AM W28455), Outer Yonge Reef, Great Barrier Reef, 14°36'S 145°38'E, rock with *Lithothamnion* & *Halimeda*, 30 m, coll. P.A. Hutchings, 24 Jan 1977.

Additional material examined. QUEENSLAND: Outer Yonge Reef, Great Barrier Reef: 14°36'S 145°38'E, rock with *Lithothamnion* & *Halimeda*, 30 m, coll. P.A Hutchings, 24 Jan 1977, 4 (AM W28962). NEW SOUTH WALES. Elisabeth & Middleton Reef, 33°16.85'S 19°9.15'E, 244 m, Franklin, May 1998; Elisabeth & Middleton Reef, 33°16.85'S 159°9.15'E, 30 m, *Lithothamnion* & *Halimeda*, 24 Jan. 77, P.A. Hutchings coll. 8 (AM W28838); Taupo Seamount, 33°16'51"S 156°09'09"E, limestone & sand bottom, 244 m, coll. J.K. Lowry, 2 May 1989, 2 (AM W28839). WESTERN AUSTRALIA Kimberley, Lafontaine Is. 68, 14°10'S 125°47'E, 9–15 m, 19 July 1988, coll. P.A. Hutchings, 1 (AM W28841).

Description. Body slender, strongly filiform, 8 mm long, 0.2 mm wide, with 50 chaetigers. Prostomium sub-pentagonal, without eyes, only 2 anterior eyespots (Fig. 56A); median antenna inserted near posterior margin of prostomium, longer than combined length of prostomium and palps; lateral antennae nearly one third length of median antenna length, similar in length to palps, inserted posteriorly to eyespots; 2 transverse furrows behind lateral antennae (Fig. 56A). Palps long, triangular, free from each other, fused basally, longer than prostomium. Peristomium distinct, about half of length of subsequent segments; dorsal tentacular cirri longer than lateral antennae but shorter than median one, similar in length to body width; ventral tentacular cirri about as long as dorsal ones (Fig. 56A). Dorsal cirri, oval, papilliform, slightly longer than parapodial lobes, without internal glands, distally tapered, absent on chaetiger 2 (Fig. 56A). Parapodial glands with granular material present on segments posterior to proventricle (Fig. 56A). Parapodial lobes elongate, conical, with distal papilla (Fig. 56D). Ventral cirri digitiform, shorter than parapodial lobes. Compound chaetae hemigomph, shafts smooth, and blades of 2 kinds; most dorsal compound chaetae with elongate, bidentate blade, short spines on margin, apparently joined by membrane on anterior and midbody parapodia (Fig. 56E,G), about 33 µm in length on anterior parapodia, 27 µm in length on midbody parapodia, 20 µm in length on posterior parapodia (Fig. 56J); remaining chaetae with shorter blades, bidentate, with short spines on margin, 15–8 µm on anterior parapodia, 10–8 µm on midbody parapodia, about 10 µm on posterior parapodia, 3 on anterior and midbody parapodia (Fig. 56F,H), 2 on posterior parapodia (Fig. 56K). Dorsal simple chaetae truncated, with few spines on margin (Fig. 56I), present from mid to posterior parapodia. Ventral simple chaetae on posterior parapodia, acicular, bidentate with both teeth hooked, proximal tooth larger than distal one, provided with small translucent hood (Fig. 56L). Solitary acicula, with oblique tip (Fig. 56M). Pharynx through 5 segments; anterior end on chaetiger 1, with small pharyngeal tooth located on anterior rim (Fig. 56A). Proventricle through two and half segments, with 30 muscle cell rows. Pygidium small, semi-circular, with 2 long, filiform anal cirri, extending for 3 segments (Fig. 56C).

Remarks. Specimens from Western Australia and Elisabeth and Middleton Reef have dorsal cirri of chaetiger 1 long and 4 small eyes are visible (Fig. 56B) and have parapodial glands larger than those present on the holotype. At this stage we prefer to regard these as variations within *Pionosyllis ancori*, as the eyes on some specimens have become faded, and cirri can easily become detached or damaged. *Pionosyllis ancori* n.sp., differs from the other Australian species of the genus in having some compound chaetae as long-bladed falcigers, long and simple dorsal chaetae truncated, and having a thread-like body. The closest species is *Pionosyllis weismanni*, which is a much more robust species, with dorsal cirri on chaetiger 2, and glands inside the dorsal cirri; the compound chaetae are similar in both species, but the ventral simple chaetae are smaller than in *P. ancori*, with the distal tooth longer and markedly curved.

Habitat. Occurring in encrusting algae and sponges, in depths of 9 to 244 m.

Distribution. Australia (Queensland, Western Australia, northern New South Wales).

Etymology. The species is named in honour to Ancor Núñez Brito, son of our friend who recently died.

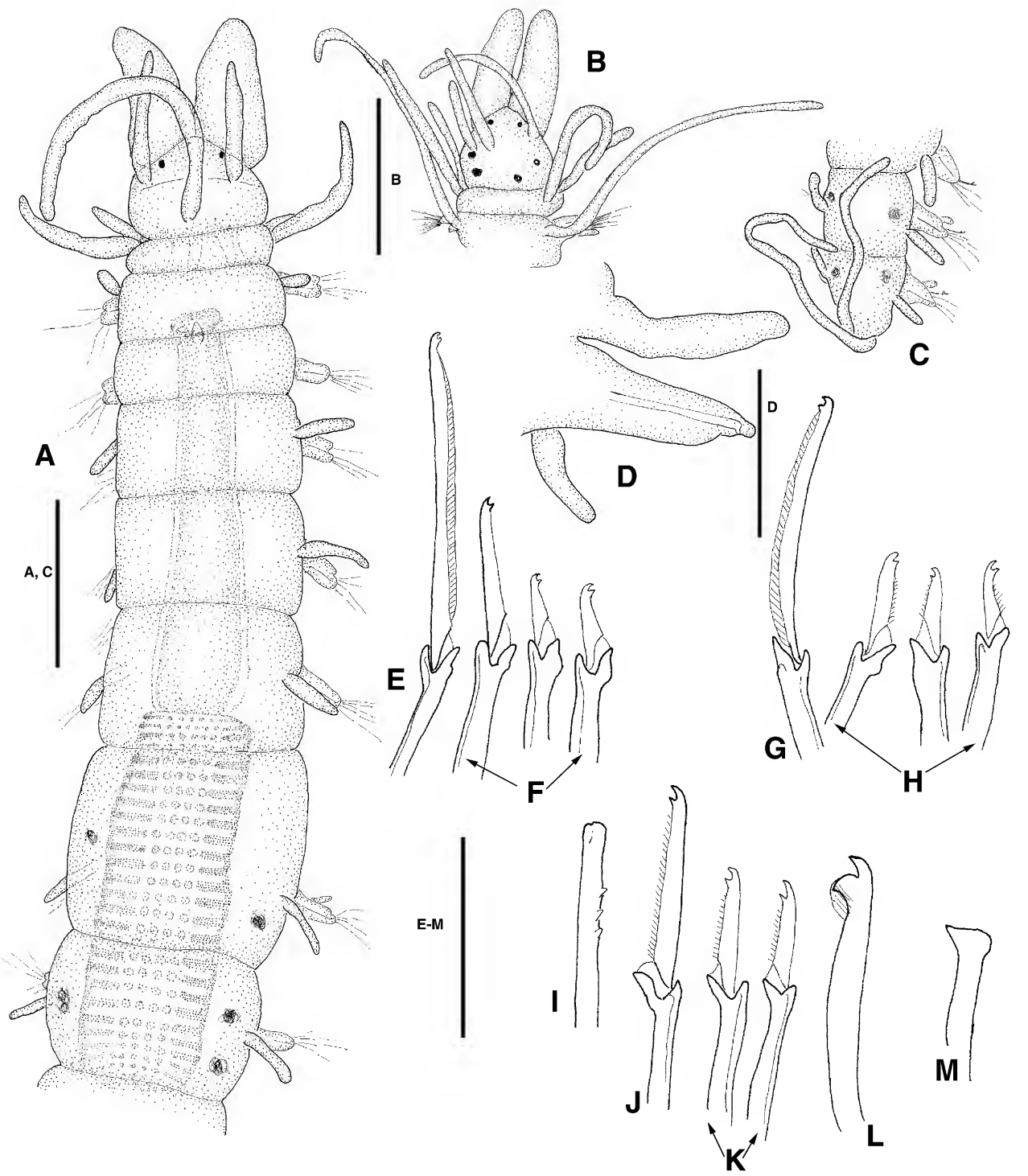


Fig. 56. *Pionosyllis ancori* n.sp. (*A*) anterior end, dorsal view; (*B*) prostomium and anteriormost segments of one specimen with long cirri on chaetiger 1; (*C*) posterior end, dorsal view; (*D*) midbody parapodium; (*E*) elongated, spiniger-like compound chaeta, anterior parapodium; (*F*) falcigers, anterior parapodium; (*G*) elongated, spiniger-like compound chaeta, midbody; (*H*) falcigers, midbody; (*I*) dorsal simple chaeta. (*J*) elongated compound chaeta, posterior parapodium; (*K*) falcigers, posterior parapodium; (*L*) ventral simple chaeta; (*M*) acicula. Scales: *A,C* 68 µm, *B* 0.18 mm, *D* 37 µm, *E–M* 20 µm. *A,C–M:* AM W29244; *B:* AM W28838.

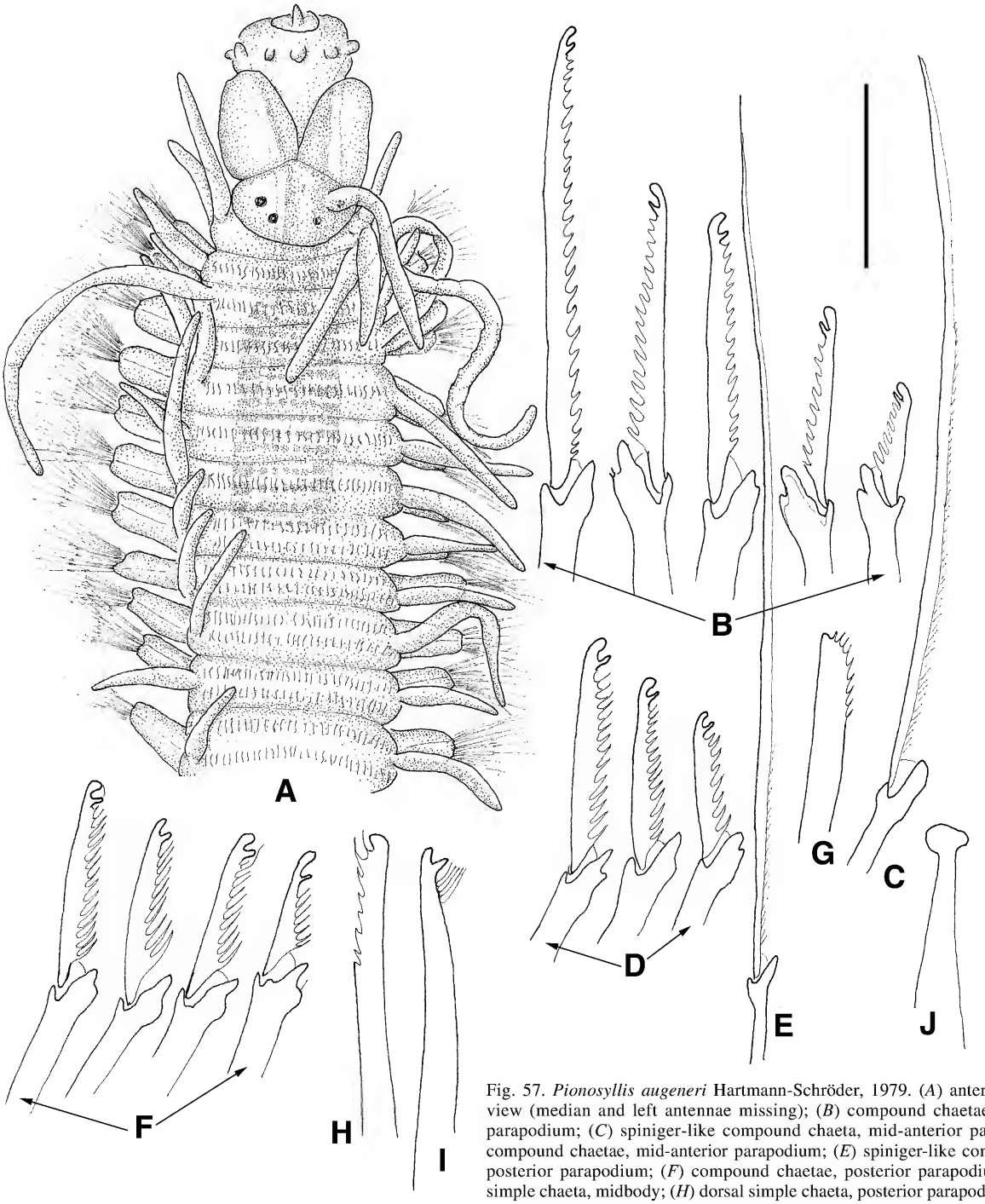


Fig. 57. *Pionosyllis augeneri* Hartmann-Schröder, 1979. (*A*) anterior end, dorsal view (median and left antennae missing); (*B*) compound chaetae, anteriormost parapodium; (*C*) spiniger-like compound chaeta, mid-anterior parapodium; (*D*) compound chaetae, mid-anterior parapodium; (*E*) spiniger-like compound chaeta, posterior parapodium; (*F*) compound chaetae, posterior parapodium; (*G*) dorsal simple chaeta, midbody; (*H*) dorsal simple chaeta, posterior parapodium; (*I*) ventral simple chaeta; (*J*) acicula, posterior parapodium. HZM P-15474. Scales: *A* 0.1 mm, *B–J* 20 µm.

Pionosyllis augeneri Hartmann-Schröder, 1979

Figs 57A–J, 58A–F

Pionosyllis augeneri Hartmann-Schröder, 1979: 98, figs 119–125; 1980: 52; 1981: 32, fig. 52. Non Hartmann-Schröder 1991: 35.

Material examined. HOLOTYPE (HMZ P-15474), PARATYPES (HMZ P-15475, P-21018, P-16796) AUSTRALIA: WESTERN AUSTRALIA: Broome, 17°58'S 122°14'E, mangrove, sand & detritus, intertidal. NEW SOUTH WALES: Palm Beach, Pittwater, 33°35'S 151°19'E, *Halophila* & *Posidonia* seagrass beds, sand, 3 m, coll. J.K. Lowry & R.T. Springthorpe, 28 Apr 1983, 3 (AM W28406) + 1 on SEM stub (AM W28898); Midstream between Juno Head & Hungry Beach, Hawkesbury R., 33°34'S 151°16'E, muddy sand, 10 m, coll. A.R. Jones & C. Watson-Russell, 12 Jan 1977, 1 (AM W22130). SOUTH AUSTRALIA: 1 km NW of 5th Creek, Port Pirie, Spencer Gulf, 33°12'S 137°55'E, 0.8 m, *Zostera*, T.J. Ward *et al*. coll, Mar 1980, 1 (AM W22106), 1 (AM W22105); Boston Bay, Port Lincoln, 34°51'S 135°51'E, washings from sheltered weedy rocks, 2 m, coll. I. Loch, 12 Feb 1985, 1 on SEM stub (AM W28880). QUEENSLAND: Halifax Bay, 19°10'S 146°44'E, 5 m, Queensland Nickel, Feb 1985, Judell, Platt, Thomas & Assoc., 2 (AM W28206). Halifax Bay, 19°10'S 146°44'E, 5 m, Queensland Nickel, Feb 1985, Judell, Platt, Thomas & Assoc., 2 (AM W28459). Triangular Islets, Shoalwater Bay, 22°23' 150°31'E, J.A. Lewis & J.R. Forsyth, 1981, 17 (AM W202630); Heron Island, 23°27'S 151°55'E, sand, intertidal, (HMZ P-21018, P-16796).

Description. Body fragile, holotype 3.8 mm long with 36 chaetigers, longest specimen 4.9 mm long, with 52 chaetigers; normally colourless, but some with black spots. Anterior part of body enlarged, after proventricle, body

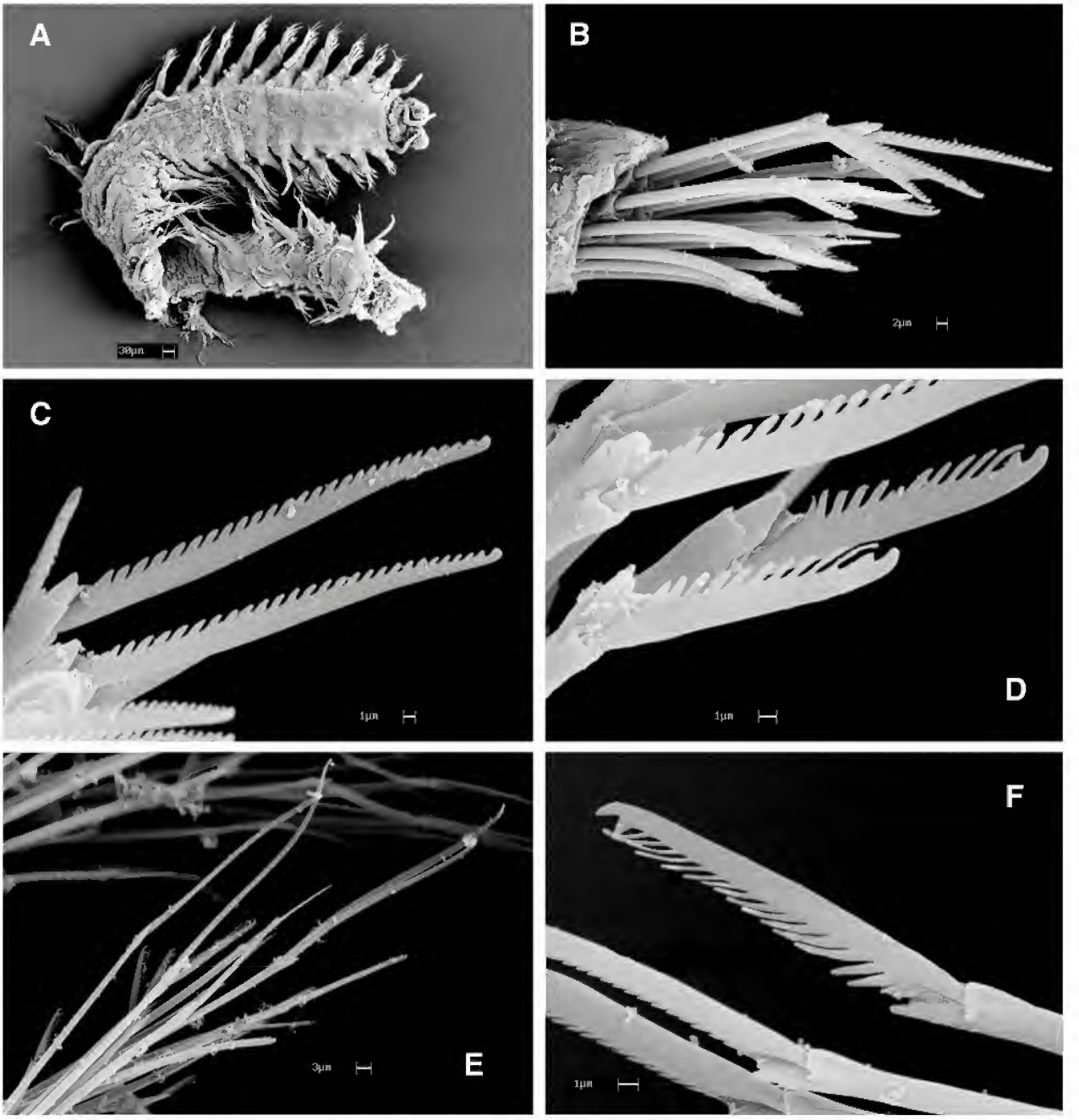


Fig. 58. SEM of *Pionosyllis augeneri* Hartmann-Schröder, 1979. (*A*) incomplete specimen, dorsal view; (*B*) anterior compound chaetae; (*C*) long, spiniger-like compound chaetae, anterior parapodium; (*D*) falcigers, midbody; (*E*) compound chaetae, midbody; (*F*) falcigers with long basal spines, posterior parapodium. AM W28898.

becoming thinner. Prostomium pentagonal, sometimes eyes absent in fixed material, but normally 4 eyes in open trapezoidal arrangement (Fig. 57A). Antennae cylindrical, smooth, long; median antenna inserted between posterior eyes, longer than combined length of prostomium and palps; lateral antennae inserted close to anterior eyes, shorter than median antenna. Palps longer than prostomium, triangular, basally fused (Figs 57A, 58A). Peristomium similar in length to subsequent segments; tentacular cirri similar to antennae; usually dorsal tentacular cirri longer than ventral tentacular cirri. Some dorsal cirri of anterior segments long, slender, filiform, others slightly shorter than body width, rest shorter than half of body width (Figs 57A, 58A); on midbody dorsal cirri alternating long and short. Parapodia of anterior segments large, subrectangular, becoming slender from proventricle segments (Fig. 57A). Ventral cirri digitiform, shorter than parapodial lobes. Anterior segments with transverse row of long cilia; from proventricular segments, 2 rows of dorsal cilia per segment (Fig. 57A). Anterior parapodia with numerous compound chaetae, about 15, with elongated blades, distally stout, with short subdistal tooth, and coarse spines on margin (Figs 57B, 58B,C), spines slightly longer on ventral chaetae (Fig. 58D); from proventricle posteriorly, some compound chaetae becoming more elongated, spiniger-like, with filiform blades, apparently unidentate (Figs 57C, 58E); other chaetae

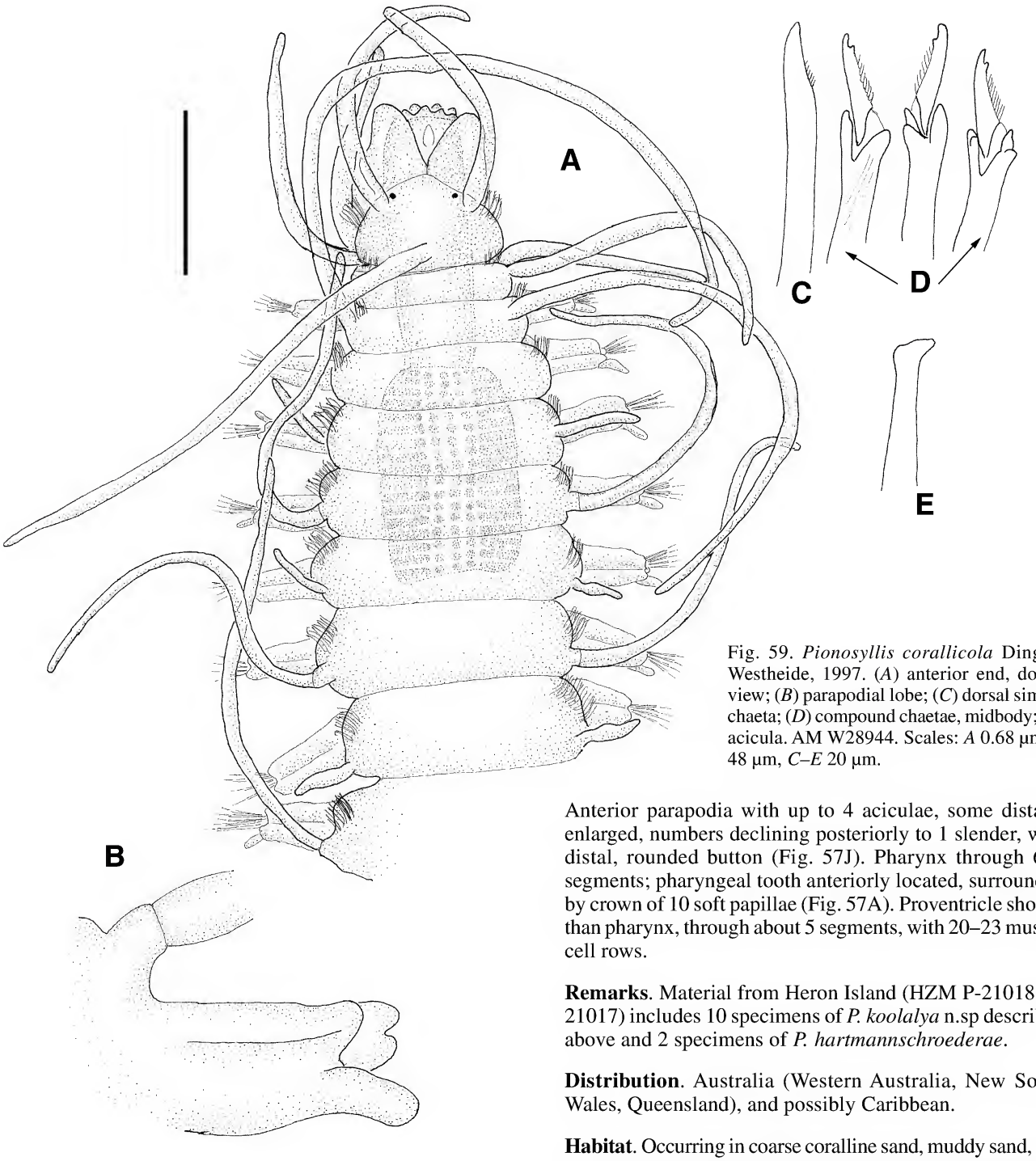


Fig. 59. *Pionosyllis corallicola* Ding & Westheide, 1997. (*A*) anterior end, dorsal view; (*B*) parapodial lobe; (*C*) dorsal simple chaeta; (*D*) compound chaetae, midbody; (*E*) acicula. AM W28944. Scales: *A* 0.68 µm, *B* 48 µm, *C–E* 20 µm.

with blades falcigerous, distally rounded, with subdistal tooth, and long spines distally directed (Fig. 57D). Posteriorly, falcigers with shorter blades, with longer and thinner spines on margin, especially basally (Fig. 57F), and longer spiniger-like chaetae (Fig. 57E). Midbody and posterior parapodia with 1 spiniger-like chaetae and 6 falcigers; posteriorly 1 spiniger-like and 4 falcigers (Figs 57F, 58F), some with long basal spines on margin. Dorsal simple chaetae from midbody, distally provided with spines of varying length (Fig. 57G), longer spines on posterior parapodia (Fig. 57H). Ventral simple chaetae on posterior parapodia, distally bidentate, both teeth similar and well separated, with some long subdistal spines (Fig. 57I). Anterior parapodia with up to 4 aciculae, some distally enlarged, numbers declining posteriorly to 1 slender, with distal, rounded button (Fig. 57J). Pharynx through 6–7 segments; pharyngeal tooth anteriorly located, surrounded by crown of 10 soft papillae (Fig. 57A). Proventricle shorter than pharynx, through about 5 segments, with 20–23 muscle cell rows.

Remarks. Material from Heron Island (HZM P-21018; P-21017) includes 10 specimens of *P. koolalya* n.sp described above and 2 specimens of *P. hartmannschroederae*.

Distribution. Australia (Western Australia, New South Wales, Queensland), and possibly Caribbean.

Habitat. Occurring in coarse coralline sand, muddy sand, and sediment in seagrasses beds, from intertidal to shallow depths.

Pionosyllis corallicola Ding & Westheide, 1997

Fig. 59A–E

Pionosyllis corallicola Ding & Westheide, 1997: 285, fig. 6.

Material examined. AUSTRALIA: WESTERN AUSTRALIA: 5 km offshore, Bush Bay, 30 km S of Carnarvon, 25°10'S 113°39'E, strap-leaved seagrass beds, 2 m, coll. J.K. Lowry & R.T. Springthorpe, 6 Jan 1984, 1 (AM W28944).

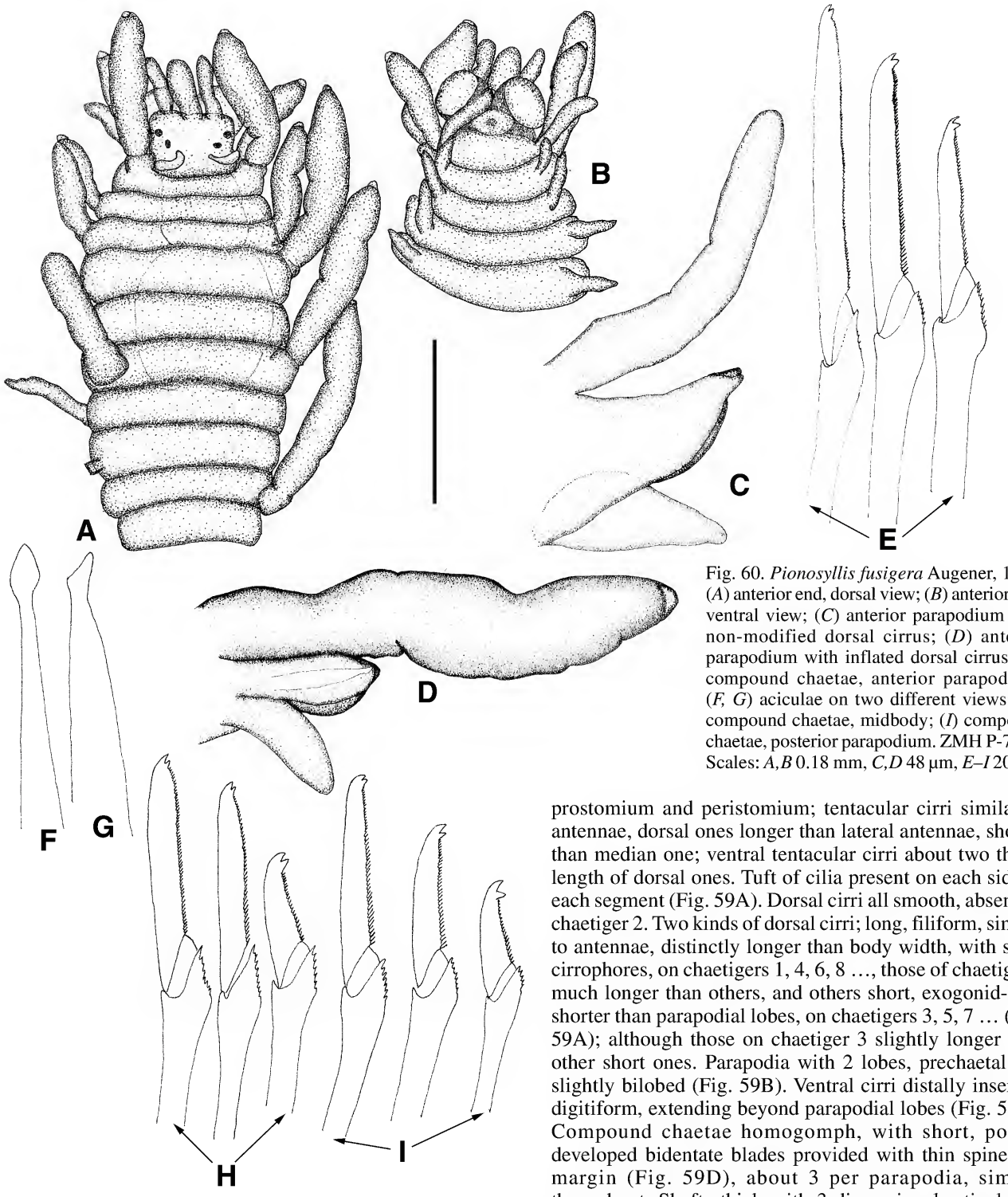


Fig. 60. *Pionosyllis fusigera* Augener, 1913. (*A*) anterior end, dorsal view; (*B*) anterior end, ventral view; (*C*) anterior parapodium with non-modified dorsal cirrus; (*D*) anterior parapodium with inflated dorsal cirrus; (*E*) compound chaetae, anterior parapodium; (*F, G*) aciculae on two different views; (*H*) compound chaetae, midbody; (*I*) compound chaetae, posterior parapodium. ZMH P-7951. Scales: *A,B* 0.18 mm, *C,D* 48 µm, *E–I* 20 µm.

Description. Body 3.6 mm long, 0.2 mm wide, with 38 chaetigers. Prostomium semi-circular to pentagonal, with 2 tufts of cilia on each side, and 2 anterior eyespots (Fig. 59A). Antennae filiform, long and slender; median antenna inserted near posterior margin of prostomium, more than 3 times combined length of prostomium and palps; lateral antennae about half of length of median antenna, inserted on anterior margin of prostomium, close to eyespots. Palps triangular to oval, similar in length to prostomium (Fig. 59A). Peristomium similar in length to following segments; nuchal organs distinct, as 2 ciliated grooves between prostomium and peristomium; tentacular cirri similar to antennae, dorsal ones longer than lateral antennae, shorter than median one; ventral tentacular cirri about two thirds length of dorsal ones. Tuft of cilia present on each side of each segment (Fig. 59A). Dorsal cirri all smooth, absent on chaetiger 2. Two kinds of dorsal cirri; long, filiform, similar to antennae, distinctly longer than body width, with short cirrophores, on chaetigers 1, 4, 6, 8 ..., those of chaetiger 1 much longer than others, and others short, exogonid-like, shorter than parapodial lobes, on chaetigers 3, 5, 7 ... (Fig. 59A); although those on chaetiger 3 slightly longer than other short ones. Parapodia with 2 lobes, prechaetal one slightly bilobed (Fig. 59B). Ventral cirri distally inserted, digitiform, extending beyond parapodial lobes (Fig. 59B). Compound chaetae homogomph, with short, poorly developed bidentate blades provided with thin spines on margin (Fig. 59D), about 3 per parapodia, similar throughout. Shafts thick with 3-dimensional articulation (Fig. 59D). Dorsal simple chaetae unidentate, thick, with few thin spines on margin (Fig. 59C). Ventral simple chaetae absent. Acicula solitary, distally expanded laterally (Fig. 59E). Pharynx through 4 segments, pharyngeal tooth on anterior rim, surrounded by crown of 10 soft papillae (Fig. 59A). Proventricle through 3 segments, with about 14 muscle cell rows. Pygidium semi-circular, with 2 filiform anal cirri.

Habitat. Occurring interstitially in coralline sand.

Distribution. China (Hainan Is.), Australia (Western Australia).

Pionosyllis fusigera Augener, 1913

Fig. 60A–I

Pionosyllis fusigera Augener, 1913: 227, pl. III Fig. 34, text-fig. 32a–c.

Material examined. Syntype 1 (HZM V-7951) AUSTRALIA: WESTERN AUSTRALIA: Sharks Bay, Surf Point, Outer Bar, 25°16'S 113°28'E, 1–3.5 m, 16 Jun 1905.

Description. Specimen in poor condition, covered with crystals of formalin. Body fragile, without colour pattern, but dark, cylindrical, flattened ventrally, convex dorsally, 4 mm long, 0.5 mm wide for 38 chaetigers, incomplete. According to Augener (1913), dorsal cirri, prostomium and palps pigmented brown and anterior segments with brown dorsal bands. Prostomium sub-quadrangular with rounded corners; 4 eyes almost equal in size, arranged in open trapezoidal pattern; 2 nuchal lobes, kidney shaped, located behind posterior pair of eyes (Fig. 60A). All antennae located on anterior margin of prostomium, short, similar in shape and size, slightly enlarged distally, as long as prostomium; lateral antennae thinner than median one (Fig. 60A). Palps broad, large, fused basally, widely separated distally, folded ventrally (Fig. 60B). Peristomial ring shorter than following segments, dorsally covered between first chaetiger and prostomium and visible only laterally and ventrally, with two pairs of tentacular cirri. Dorsal tentacular cirri and some dorsal cirri similar in shape, smooth, thick, club-shaped, basally slender and gradually becoming wider distally, terminating in globular papillae; most anterior cirri slightly shorter than middle and posterior cirri (Fig. 60B); ventral tentacular cirri similar in shape and size to lateral antennae. Long, club-shaped dorsal cirri alternating with shorter, thinner, digitiform cirri, as long as half of body width (Fig. 60A). Ventral cirri conical to digitiform, distally pointed, almost as long as parapodia. Parapodia with prechaetal lobe larger than postchaetal one (Fig. 60C,D). Compound chaetae heterogomph falcigers; shafts with distal short spines; blade tips bidentate, distal tooth hooked, proximal tooth similar in size to distal one (Fig. 60E,H,I). About 12 compound chaetae on anterior parapodium, number progressively decreasing posteriorly; dorsalmost compound chaetae on each parapodium with elongate, slender, minutely bidentate blade, with numerous fine, short spines on edge, 60 μm in length on anterior parapodia, shorter, about 36 μm in length, posteriorly. Blades of remaining chaetae more strongly bidentate, all similar in shape with slight dorsoventral and anteroposterior gradation in size, blades progressively becoming shorter and wider posteriorly, about 54 μm in length dorsally and 28 μm in length ventrally on anterior parapodia; blades on posterior parapodia about 31 μm in length dorsally and 20 μm in length ventrally (Fig. 60H,I). Anterior parapodia with 2 straight, thick, acuminate, distally pointed aciculae; posterior parapodia with single acicula (Fig. 60F,G). Pharynx, removed from specimen, reaching segment 4, pharyngeal tooth on segment 2 (fide Augener, 1913). Proventricle barrel shaped, extending through 3 chaetigers (from 4 to 7) (Fig. 60A) with about 18 muscle cell rows.

Habitat. Occurring in depths of 1 to 3.5m.

Distribution. Australia (Western Australia).

Pionosyllis hartmannschroederae n.nom.

Fig. 61A–F

Typosyllis (Langerhansia) longisetosa Hartmann-Schröder, 1990: 49, figs 9–12.

Pionosyllis augeneri.—Hartmann-Schröder, 1991: 35. Not Hartmann-Schröder, 1979: 98.

Material examined. AUSTRALIA: NEW SOUTH WALES: Angourie Point, 29°29'S 153°22'E, algal beds, intertidal, holotype of *Typosyllis (Langerhansia) longisetosa*, (HZM P-19661), paratype (HZM P-19962). WESTERN AUSTRALIA: Goss Passage, Beacon Is., 28°25.5'S 113°47'E, dead coral substrate, in fine sediment at foot of reef slope, P.A Hutchings, 23 May 1994, 4 (AM W28386); NE entrance to Goss Passage, Beacon Is, 28°27.9'S 113°46.7'E, terebellids on rocks in coral sand at foot of slope, 33 m, P.A. Hutchings, 25 May 1994. 1 (AM W26455); inshore limestone reef, Ned's Camp, Cape Range National Park, 21°59'S, fine sediment & sand from patches between reefs, H.E. Stoddart, 2 Jan 1984, 4 (AM W26785); 5 km offshore Bush Bay, 30 km S of Carnarvon 25°10'S 113°55'E, shallow strap-leaved seagrass beds, 2 m, coll. J.K. Lowry & R.T. Springthorpe, 6 Jan 1984, 1 (AM W28926); Descartes Is., Kimberleys, 14°11'S 125°40'E, sandflats & mangroves, coll. P.A. Hutchings, 20 July 1988, 1 (AM W28397).

Description. Body 1.4 mm long, 0.2 mm wide, with 53 chaetigers. Prostomium oval to circular, with 4 eyes in open trapezoidal arrangement (Fig. 61A), absent in some specimens (probably lost after fixation); median antenna about two and half times longer than combined length of prostomium and palps, inserted between posterior eyes; lateral antennae slightly shorter than median antenna, inserted near anterior margin. Palps broad, longer than prostomium (Fig. 61A). Peristomium shorter than following segments; dorsal tentacular cirri elongated, filiform, similar to median antenna, ventral tentacular cirri smaller. Dorsal cirri elongate, slender, smooth, filiform, varying in length in different specimens and in each specimen, some cirri long, several times longer than body width, and some cirri shorter than body width, alternating irregularly (Fig. 61A). Anterior parapodia broad, becoming conical and slender from proventricle segments onwards. Ventral cirri digitiform, shorter than parapodial lobes anteriorly, elongated on posterior parapodia, longer than parapodial lobes. Compound chaetae similar throughout, including 1–2 long, slender, filiform spiniger-like chaetae, 180 μm in length, 1–2 falcigers with bidentate blades, provided with long spines on margin, especially basally, and distal spines extending beyond level of distal tooth, straight margin of blade with convex curvature proximally then concave subdistally (Fig. 61C), 45–47 μm in length, and about 5 chaetae with bidentae blades, with long distal spines, and short basal spines (Fig. 61D) and dorsoventral gradation in length within fascicle, 40 μm in length dorsally, 25 μm in length ventrally. Dorsal simple chaetae from proventricle segments, with distinct, short spines on margin (Fig. 61E). Ventral simple chaetae on posterior segments, distinctly bidentate, proximal tooth prominent, slightly longer than distal tooth, and some thin spines on margin, distal one longer than others, extending to level of distal tooth. Aciculae distally knobbed, with 2 lateral, unequal lobes (Fig. 61F); 2 aciculae on anterior parapodia. Pharynx slender, through about 6–7 segments (Fig. 61A). Proventricle through 4–6 segments, with about 24 muscle cell rows. Pygidium small, with 2 filiform anal cirri.

Remarks. Hartmann-Schröder described two different species named *longisetosa* in two different genera, on the

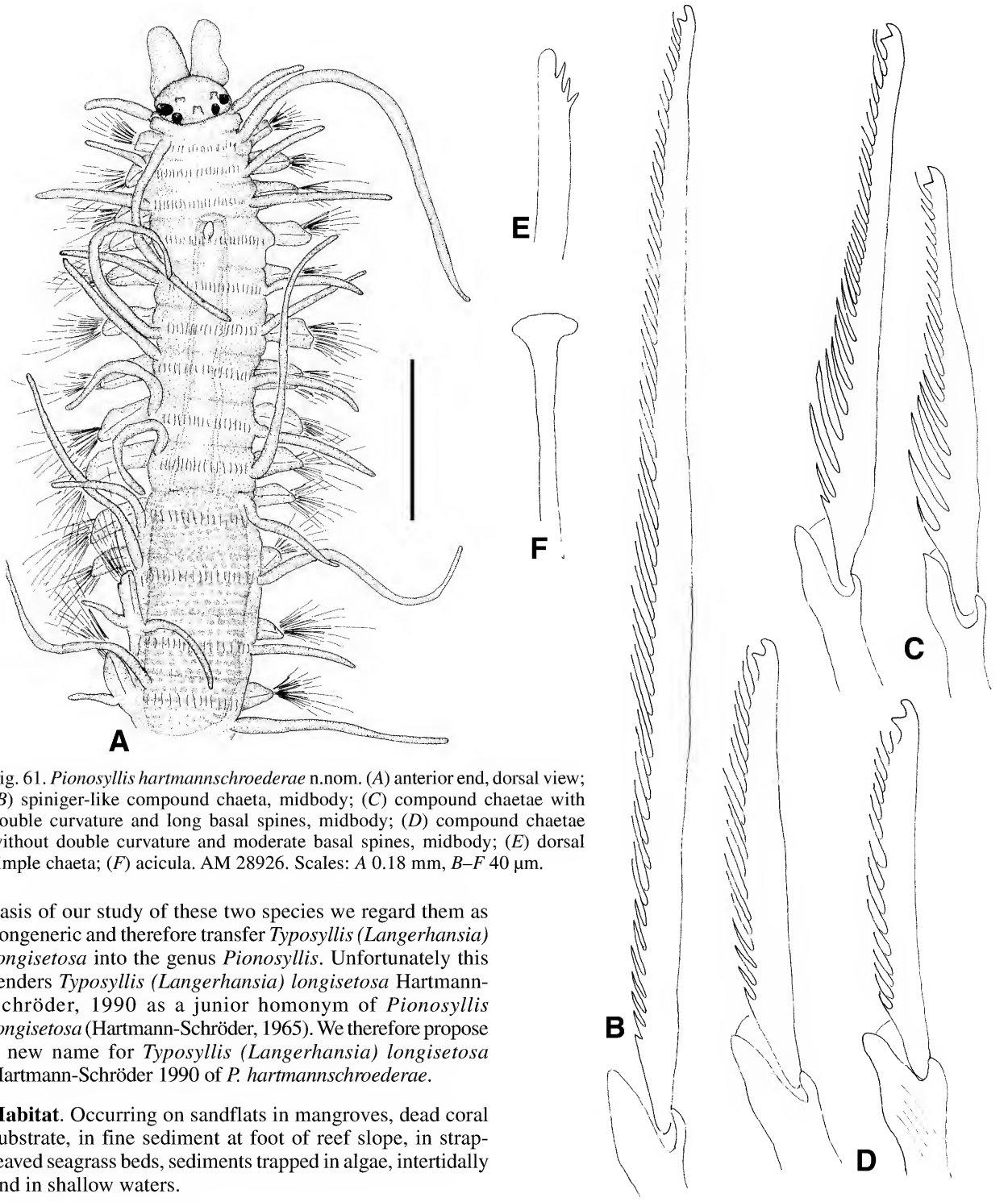


Fig. 61. *Pionosyllis hartmannschroederae* n.nom. (*A*) anterior end, dorsal view; (*B*) spiniger-like compound chaeta, midbody; (*C*) compound chaetae with double curvature and long basal spines, midbody; (*D*) compound chaetae without double curvature and moderate basal spines, midbody; (*E*) dorsal simple chaeta; (*F*) acicula. AM 28926. Scales: *A* 0.18 mm, *B–F* 40 μm.

basis of our study of these two species we regard them as congeneric and therefore transfer *Typosyllis (Langerhansia) longisetosa* into the genus *Pionosyllis*. Unfortunately this renders *Typosyllis (Langerhansia) longisetosa* Hartmann-Schröder, 1990 as a junior homonym of *Pionosyllis longisetosa* (Hartmann-Schröder, 1965). We therefore propose a new name for *Typosyllis (Langerhansia) longisetosa* Hartmann-Schröder 1990 of *P. hartmannschroederae*.

Habitat. Occurring on sandflats in mangroves, dead coral substrate, in fine sediment at foot of reef slope, in strap-leaved seagrass beds, sediments trapped in algae, intertidally and in shallow waters.

Distribution. Australia (Queensland, Western Australia).

Pionosyllis heterochaetosa n.sp.

Figs 62D–F, 63A–O, 64A–F

Material examined. HOLOTYPE (AM W21629) AUSTRALIA: NEW SOUTH WALES: S of airport runway extension, Botany Bay, 33°58.13'S 151°11.16'E, muddy sand, 5 m, coll. Australian Museum party, 6 Apr 1992. PARATYPES S of airport runway extension, Botany Bay, 33°58.13'S 151°11.16'E, muddy sand, 5 m, Australian Museum party, 27 July 1992, 3 on SEM stub (AM W22117); S of airport runway extension, Botany Bay, 33°58.10' 151°11.16'E, muddy sand, 5 m, coll. Australian Museum party, 27 July 1992, 2 (AM W22110); S of airport runway extension, Botany Bay, 33°58.13'S 151°11.16'E, muddy sand, 5 m, Australian Museum party, 6 Apr 1992, 2 (AM W22112); S of airport runway extension, Botany Bay, 33°58.13'S 151°11.16'E, muddy sand, 5 m, coll. Australian Museum party, 27 July 1992, 1 on SEM stub (AM W22116). S of airport runway extension, Botany Bay, 33°58.13'S 151°11.16'E, muddy sand, 5 m, coll. Australian Museum party, 27 July 1992, 2 (AM W22115).

Description. Body 4.6 mm long, 0.2 mm wide, with 54 chaetigers. Prostomium circular, with 4 eyes in open trapezoidal arrangement (Fig. 63A); median antenna long, about 3 times longer than combined length of prostomium and palps, inserted between posterior eyes; lateral antennae

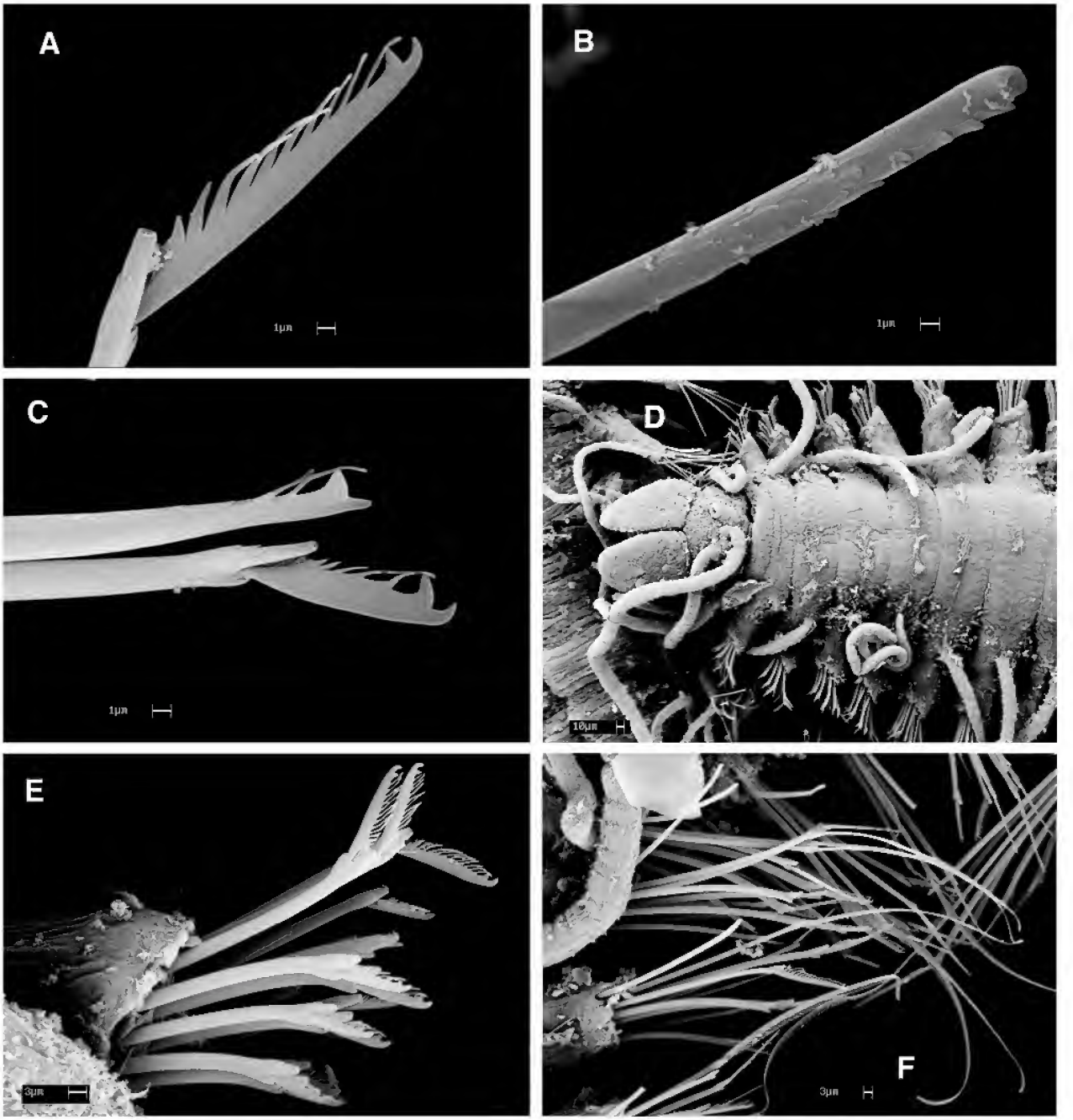


Fig. 62. SEM of *Pionosyllis koolalya* n.sp. (*A*) compound chaeta, midbody; (*B*) dorsal simple chaeta; (*C*) ventral simple chaeta and falciger, posterior parapodium. SEM of *Pionosyllis heterochaetosa* n.sp. (*D*) anterior end, dorsal view; (*E*) compound chaetae, anterior parapodium; (*F*) fascicles of chaetae, midbody. *A–C*: paratype, AM W28409; *D–F*: paratype, AM W22117.

about half or third length of median antenna, inserted near anterior margin. Palps broad, longer than prostomium (Figs 62D, 63A). Peristomium shorter than subsequent segments; dorsal tentacular cirri elongated, filiform, similar to median antenna, ventral tentacular cirri smaller. Dorsum of anterior segments each with transverse band of cilia (Figs 62D, 63A); double row from proventricle segments onwards. Dorsal cirri elongated, slender, smooth, filiform, varying in length in different specimens and in each specimen, some cirri long, several times longer than body width, and some cirri shorter than body width, alternating irregularly (Figs 62D, 63A). Anterior parapodia broad, becoming conical and slender from proventricle segments posteriorly. Ventral cirri digitiform, shorter than parapodial lobes anteriorly, elongated on posterior parapodia, longer than parapodial lobes. Most anterior parapodia with numerous compound chaetae, about 10–15, slightly enlarged shafts, and short, bidentate blades, provided with long spines on margin (Figs 62D,E, 63B), especially on more dorsal chaetae, extending beyond distal tooth, and dorsoventral gradation in length within fascicle, about 16 µm in length dorsally, 5–6 µm in length ventrally. Progressively along body, number of compound chaetae per parapodium decreasing, and blades of more dorsal compound chaetae becoming elongate and more strongly bidentate (Fig. 63C); on chaetiger 5, blades about 22 µm in length dorsally, 12 µm in length ventrally. From proventricular segments, parapodia with 2–3, sometimes only 1, compound chaetae with elongate,

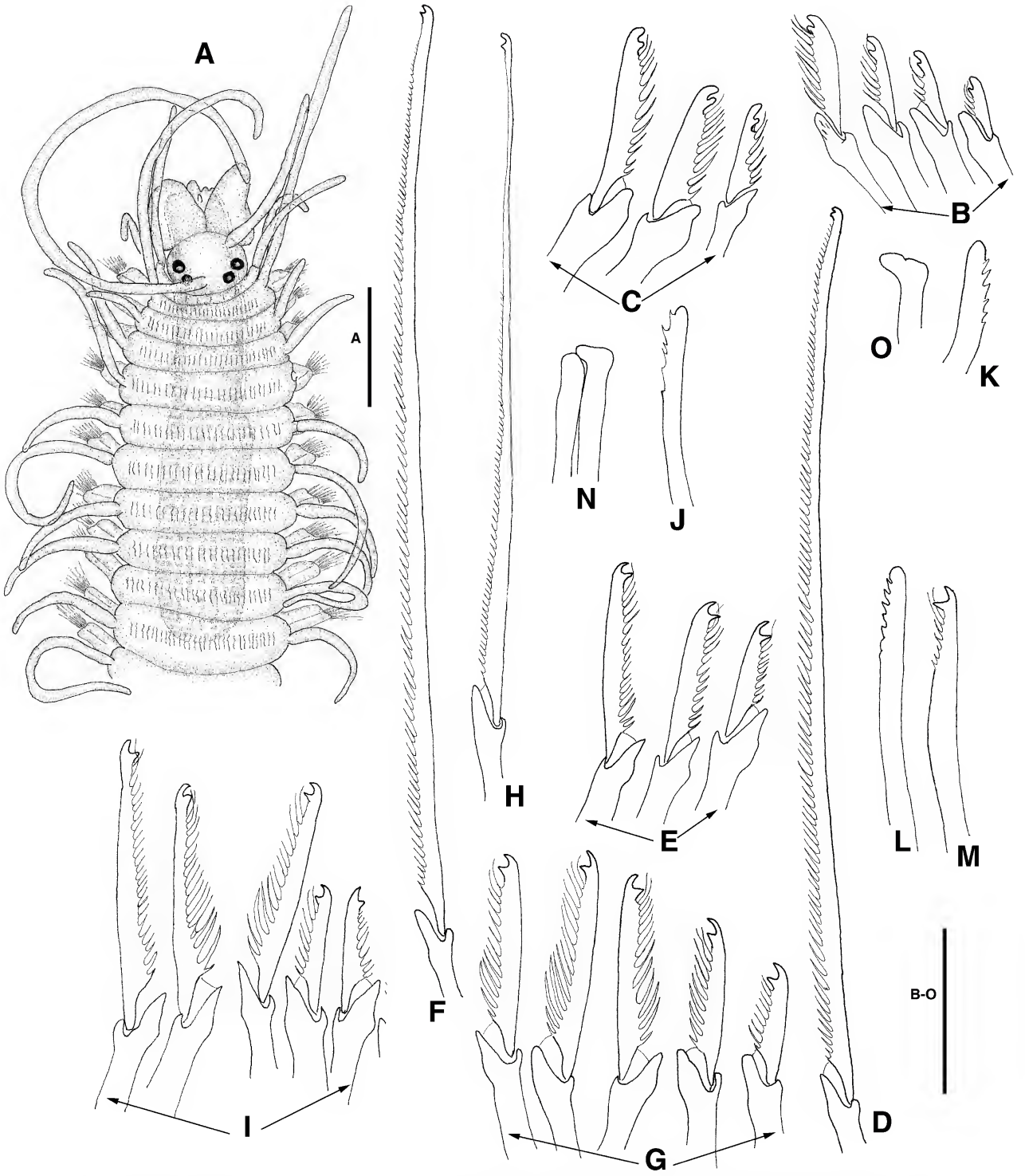


Fig. 63. *Pionosyllis heterochaetosa* n.sp. (*A*) anterior end, dorsal view; (*B*) compound chaetae, anteriormost parapodium; (*C*) compound chaetae, anterior parapodium; (*D*) spiniger-like compound chaeta, mid-anterior parapodium; (*E*) compound chaetae, mid-anterior parapodium; (*F*) spiniger-like compound chaeta, midbody; (*G*) compound chaetae, midbody; (*H*) spiniger-like compound chaeta, posterior parapodium; (*I*) compound chaetae, posterior parapodium; (*J*) dorsal simple chaeta, anterior parapodium; (*K*) same, midbody; (*L*) same, posterior parapodium; (*M*) ventral simple chaeta; (*N*) aciculae, anterior parapodium; (*O*) acicula, posterior parapodium. AM W21629 (holotype). Scales: *A* 0.18 mm, *B–O* 20 μm.

spiniger-like blades (Fig. 62F), about 112 μm in length, weakly bidentate distally, with moderate spines on margin (Fig. 63D,F,H), and 5–6 compound chaetae with falcigerous, bidentate blades, slender, margin with long, distinct, distally pointed basal spines and thin, fine, spines distally (Figs 62F, 63E,G,I, 64B–D), reaching level of distal tooth, and dorsoventral gradation in length within fascicle, 25 μm dorsally, 15 μm ventrally. Dorsal simple chaetae from proventricle segments, distally broad, provided with short spines on margin (Figs 63J–L, 64E). Ventral simple chaetae on posterior segments, bidentate, proximal tooth prominent, slightly longer than distal tooth, and some thin spines on margin, 2–3 distal ones longer than others, reaching to level of distal tooth (Figs 63M, 64F). Aciculae distally knobbed, with 2 lateral, unequal lobes (Fig. 63 O); 2 aciculae on anterior parapodia (Fig. 63N). Pharynx slender, through

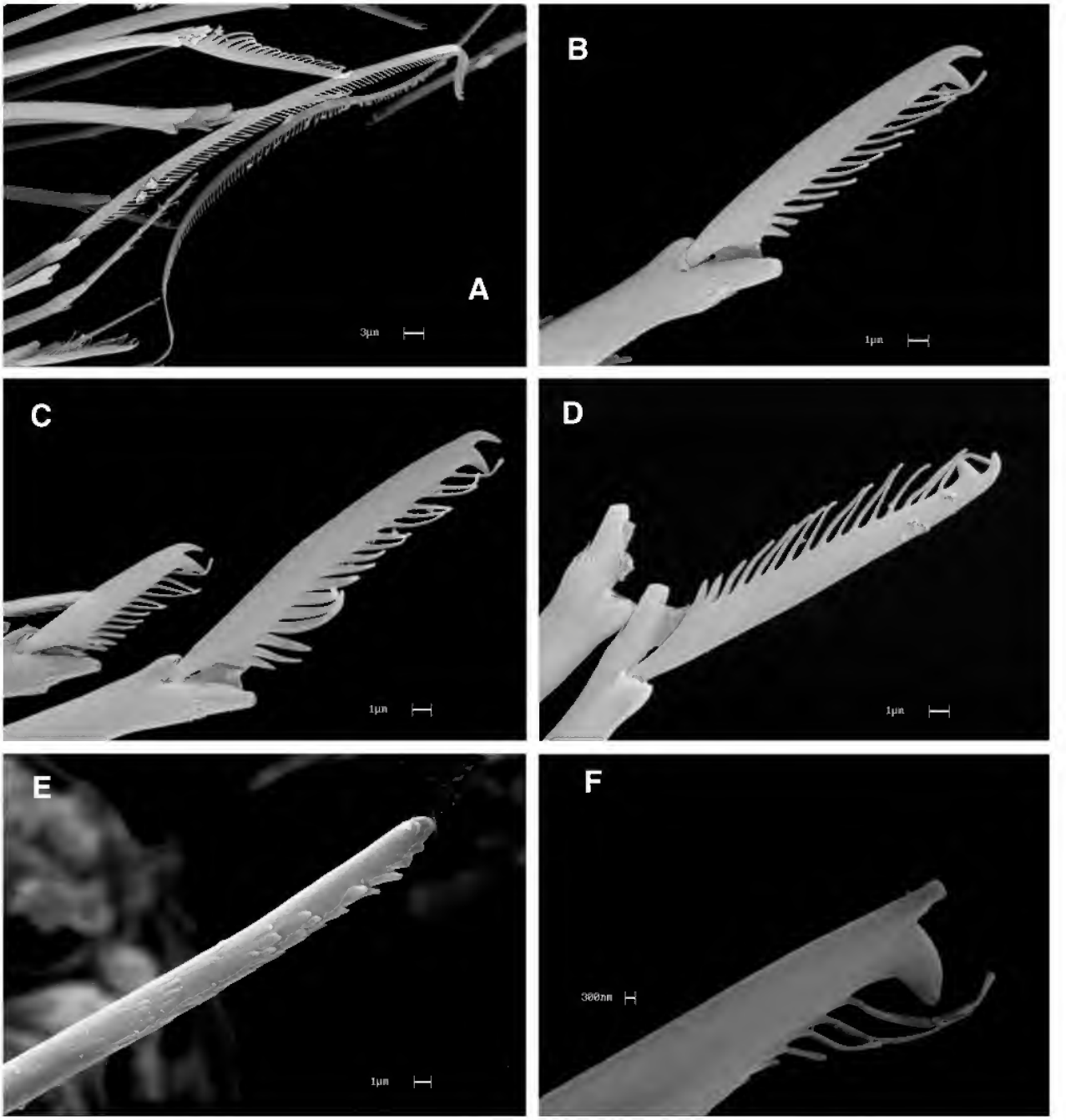


Fig. 64. SEM of *Pionosyllis heterochaetosa* n.sp. (*A*) chaetae, midbody; (*B–D*) compound chaetae, midbody; (*E*) dorsal simple chaeta; (*F*) ventral simple chaeta. AM W22116, AM W22117.

about 6–7 segments (Fig. 63A). Proventricle through 6 segments, with about 24 muscle cell rows. Pygidium small, with 2 filiform anal cirri.

Remarks. *Pionosyllis heterochaetosa* n.sp. is characterized by having anterior parapodia without spiniger-like compound chaetae, which appear in post- proventricle segments. *Pionosyllis serrata* and *P. koolalya*, described above, also lack spiniger-like chaetae anteriorly, and posteriorly. All other species of the genus (*P. hartmann-schroederae* and *P. augeneri* described below, as well as *P. spinisetosa* San Martín, 1990, from Cuba, and *P. anophthalma* Capaccioni & San Martín, 1989, from the western Mediterranean Sea), have spiniger-like compound chaetae from chaetiger 1 (see San Martín, 1990, 2003), as well as *P. longisetosa* (Hartmann-Schröder, 1965) from Chile (see Hartmann-Schröder, 1965).

Distribution. Australia (New South Wales).

Habitat. Occurring in muddy sand at about 5 m depth.

Etymology. The specific name refers to the presence of different chaetae on anterior segments compared to others.

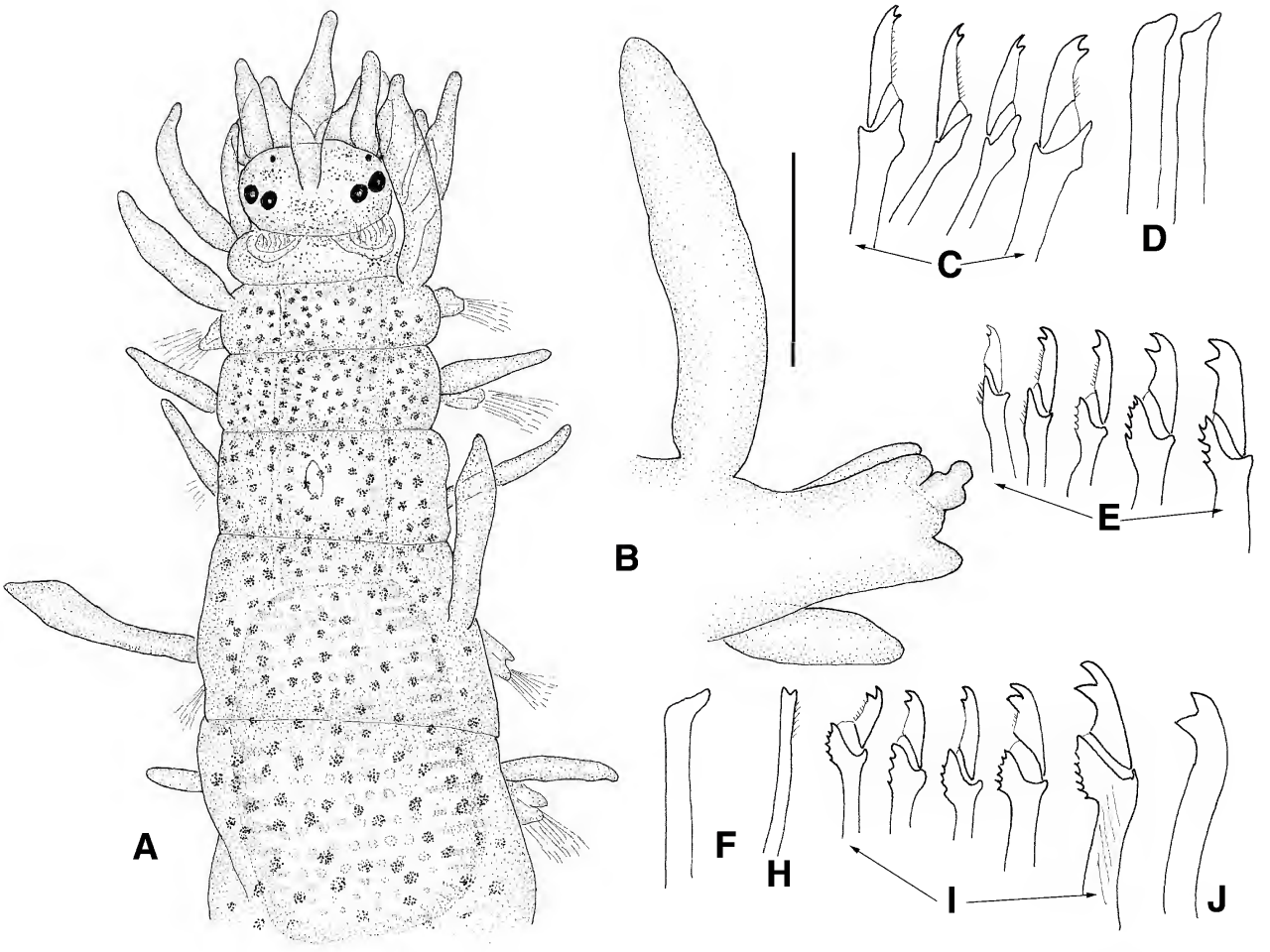


Fig. 65. *Pionosyllis kalimna* n.sp. (*A*) anterior end, dorsal view; (*B*) midbody parapodium; (*C*) compound chaetae, anterior parapodium; (*D*) aciculae, anterior parapodium; (*E*) compound chaetae, midbody; (*F*) acicula, midbody; (*G*) posterior end, dorsal view; (*H*) dorsal simple chaeta; (*I*) compound chaetae, posterior parapodium; (*J*) ventral simple chaeta; (*K*) acicula, posterior parapodium. AM W28948. Scales: *A,G* 0.18 mm; *B* 48 µm; *C–F, H–K* 20 µm.

***Pionosyllis kalimna* n.sp.**

Fig. 65A–K

Material examined. HOLOTYPE (AM W28948) AUSTRALIA: WESTERN AUSTRALIA: N end of beach, Bundegi Reef, Exmouth Gulf, 21°49'S 114°11'E, rocky rubble, sediment & brown algae with epiphytes, 2 m, coll. H.E. Stoddart, 4 Jan 1984. PARATYPES 2 (AM W26779) N end of beach, Bundegi Reef, Exmouth Gulf, 21°49'S 114°11'E, rocky rubble, coralline algae with green epiphyte, 2 m, coll. H.E. Stoddart, 4 Jan 1984.

Description. Body 6.4 mm long, 0.3 mm wide, slightly broad anteriorly, tapering posteriorly, with 39 chaetigers plus 5–6 segments without chaetae (Fig. 65A,G), darkly pigmented prostomium and peristomium, anterior segments covered in numerous red pigment spots (Fig. 65A). Prostomium oval to rectangular, with 4 eyes in open trapezoidal arrangement and 2 anterior eyespots; median antenna inserted between anterior eyes, on middle of prostomium, fusiform, slightly longer than combined length of prostomium and palps; lateral antennae similar to median antenna but less fusiform, inserted in front of anterior margin of prostomium, ventral in relation to median antenna, slightly longer than palps. Palps triangular, divergent, free for most of length, fused basally, slightly shorter than prostomium (Fig. 65A). Peristomium similar in length to subsequent segments, with 2 nuchal organs forming ciliated dorsal pits; dorsal tentacular cirri similar in shape and length to median antenna, ventral tentacular cirri similar to lateral ones. Median antenna, dorsal tentacular cirri, and dorsal cirri of chaetigers 1, 4, and 6, enlarged, fusiform, distinctly longer than remaining appendages (Fig. 65A); remaining dorsal cirri not as fusiform, and shorter, about two thirds length of longer ones. Parapodia with bilobed prechaetal lobe and trilobed postchaetal lobe, medium lobe enlarged at base with rounded tip (Fig. 65B). Ventral cirri digitiform, shorter than parapodial lobes. Compound chaetae heterogomph, with smooth or nearly smooth shafts

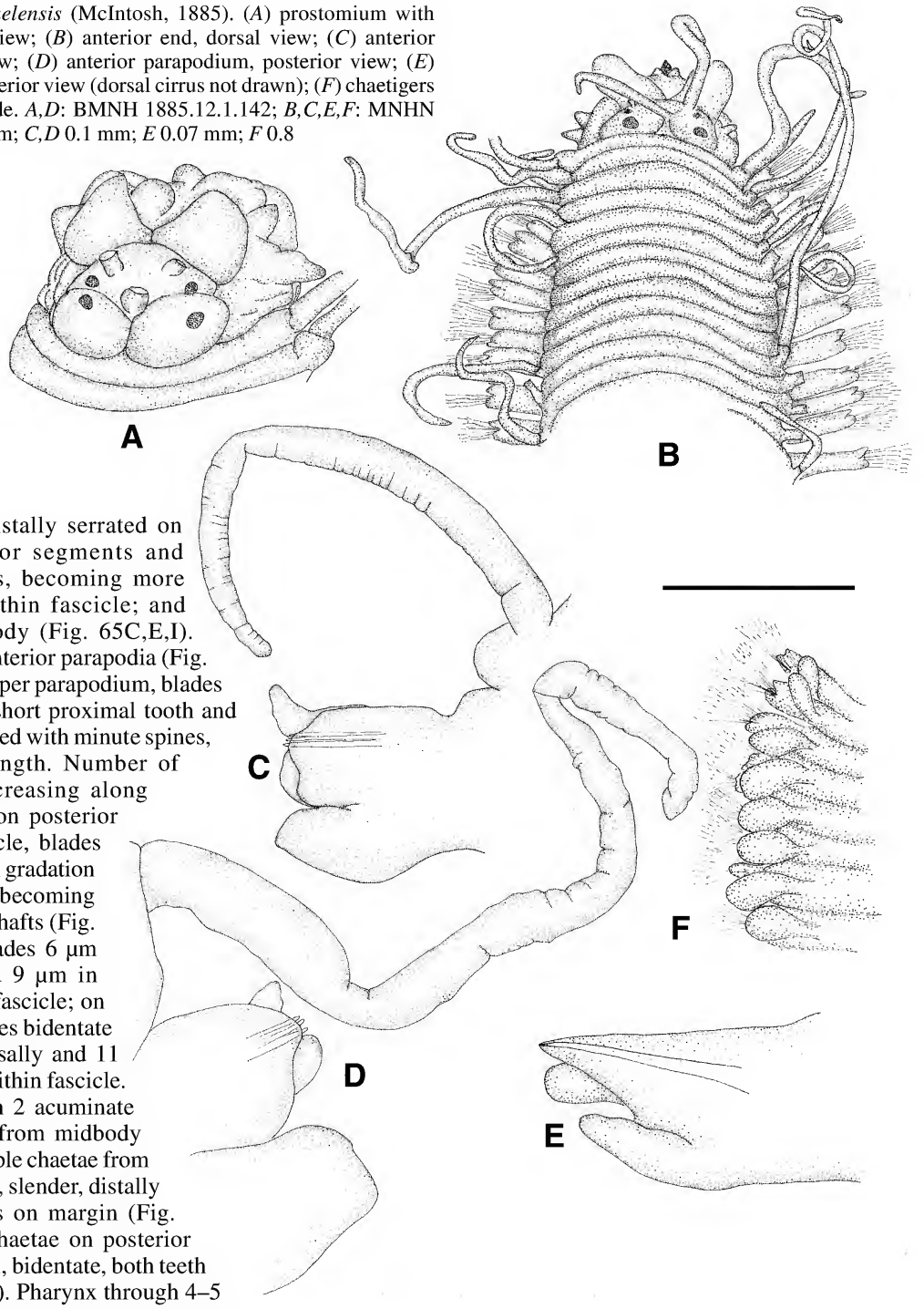


Fig. 66. *Pionosyllis kerguelensis* (McIntosh, 1885). (*A*) prostomium with everted pharynx, dorsal view; (*B*) anterior end, dorsal view; (*C*) anterior parapodium, posterior view; (*D*) anterior parapodium, posterior view; (*E*) posterior parapodium, posterior view (dorsal cirrus not drawn); (*F*) chaetigers 1–8, ventral view, right side. *A,D*: BMNH 1885.12.1.142; *B,C,E,F*: MNHN A-921. Scales: *A,B* 0.56 mm; *C,D* 0.1 mm; *E* 0.07 mm; *F* 0.8

anteriorly becoming distally serrated on midbody and posterior segments and bidentate, short blades, becoming more bidentate ventrally within fascicle; and progressively along body (Fig. 65C,E,I). Compound chaetae of anterior parapodia (Fig. 65C) all similar, about 7 per parapodium, blades relatively slender with short proximal tooth and smooth margin or provided with minute spines, about 10–11 µm in length. Number of compound chaetae increasing along body, up to 9 present on posterior parapodia; within fascicle, blades with inverse dorsoventral gradation in length, terminal teeth becoming larger and with thicker shafts (Fig. 65E,I), on midbody, blades 6 µm in length dorsally and 9 µm in length ventrally within fascicle; on posterior parapodia blades bidentate and 6 µm in length dorsally and 11 µm in length ventrally within fascicle. Anterior parapodia with 2 acuminate aciculae (Fig. 65D), 1 from midbody (Fig. 65F,K). Dorsal simple chaetae from mid-posterior parapodia, slender, distally bifid, with short spines on margin (Fig. 65H). Ventral simple chaetae on posterior parapodia, thick, smooth, bidentate, both teeth well separated (Fig. 65J). Pharynx through 4–5 segments; pharyngeal tooth inserted posteriorly to mid pharynx (Fig. 65A), on chaetiger 3. Proventricle through 2 segments, large, with about 30 muscle cell rows, difficult to count. Pygidium semi-circular, with 2 oval, slightly enlarged, anal cirri, slightly longer than pygidium (Fig. 65G).

Remarks. *Pionosyllis kalimna* n.sp. is easily distinguished from *P. fusigera* Augener, 1913, by the compound chaetae that are short with two equally well-developed terminal teeth, enlarged dorsal cirri without a distal button; it also differs in the structure of the parapodia, and the colour pattern, black stripes in *P. fusigera*, and small red spots in *P. kalimna*.

Habitat. Occurring in rocky rubble, sediment and brown algae with epiphytes, in 2 m depth.

Distribution. Australia (Western Australia).

Etymology. The specific name comes from an aboriginal word, *kalimna* meaning beautiful.

Pionosyllis kerguelensis (McIntosh, 1885)

Figs 66A–F, 67A–L

Eusyllis kerguelensis McIntosh, 1885: pl. 29, fig. 4, pl. 33 fig. 3, Pl. 15a fig. 13. Ehlers, 1897: 42; 1913: 473.—Augener, 1924: 376; 1927: 152.—Monro, 1930: 94, fig. 30a-c; 1936: 130.—Knox, 1951: 73; 1960: 105.—Knox & Cameron, 1998: 49, figs 99–100.—Hartman, 1953: 20; 1964: 81, pl. 25, figs 2–3.—Wesenberg-Lund, 1961: 59, fig. 19.—Hartmann-Schröder, 1965: 115, figs 74; 1986: 77.—Averincev, 1982: 19, pl. II, Figs 1–2.—Hartmann-Schröder & Rosenfeldt, 1988: 39, fig. 16; 1990: 97; 1992: 98.

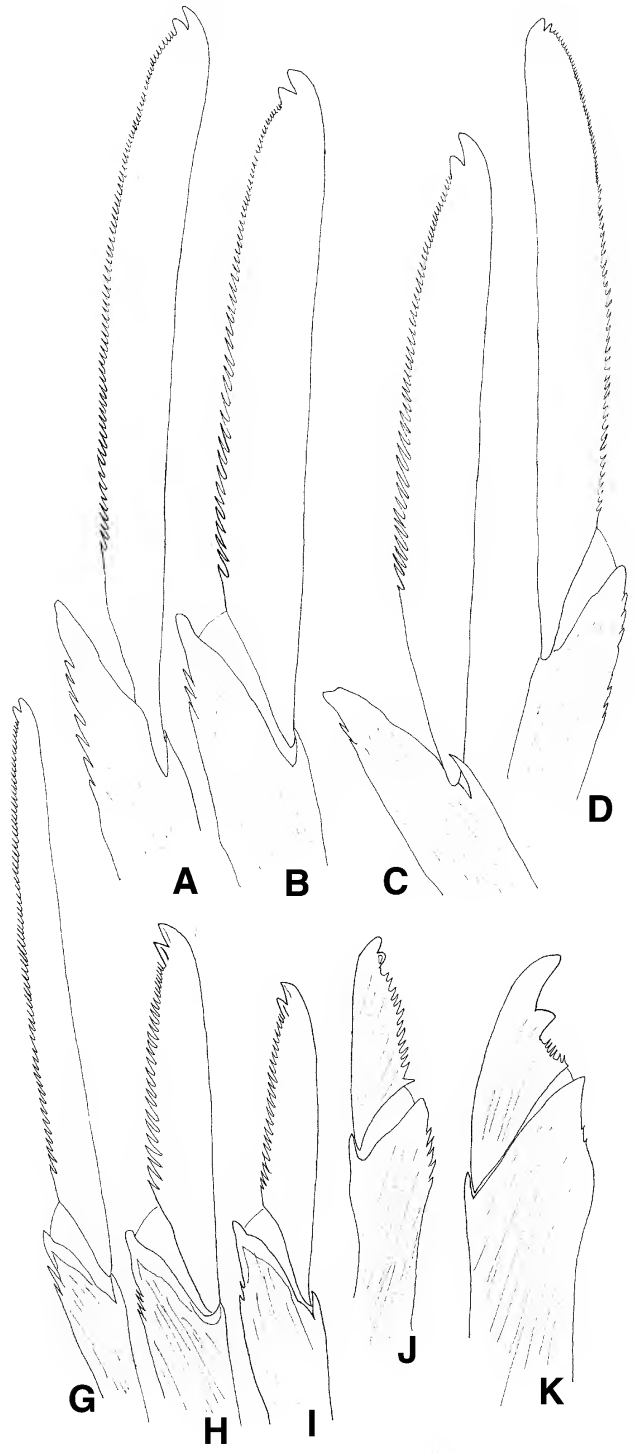
Pionosyllis comosa Gravier, 1906: 288.—Ehlers, 1913: 473, pl.32, Figs 1–4.—Benham, 1927: 60.—Monro, 1930: 92; 1936: 128, fig. 20.—Hartman, 1953: 23; 1964: 85, pl. 26 figs 7–8; 1967: 58.

Pionosyllis cosma [sic] Knox, 1960: 106.—Knox & Cameron 1998: 51.

Pionosyllis kerguelensis San Martín & Parapar, 1997: 291; San Martín, 2004: 16.

Material examined. KERGUELEN IS. off Christmas harbour, 49°30'S 69°30'W, 200 m, coll. H.M.S. Challenger, presented McIntosh, syntype of *Eusyllis kerguelensis*, BMNH 1885.12.1.142 (1 ant. end + 2 median parts). FALKLAND ISLANDS: Port Albemarle, 52°11'S 60°26'W, 40 m, sand & algae, coll. Swedish Antarctic Exp. 1901–1903, 8 Sept. 1902, *Pionosyllis comosa*, 2 (SMNH 3332, 3728); Burwood bank, 53°45'S 61°10'W, 137–150 m, shell fragments & stones, coll. Swedish Antarctic Exp. 1901–1903, 12 Sept. 1902, *P. comosa* 1 (SMNH 3660). ARGENTINA: coast of northern Argentina: 37°15'S 56°8'W, 100 m, sand & gravel, coll. Swedish Antarctic Exped. 1901–1903, 23 Dec 1901, *P. comosa* 1 (SMNH 3826). SOUTH GEORGIA: south fjord in front of Nordenskjöld glacier, 54°24'S 36°22'W, 210 m, blue grey mud with few small stones, coll. Swedish Antarctic Exp. 1901–1903, 29 May 1902, *Pionosyllis epipharynx* 1 (SMNH 3033); French Antarctic Exp. Charcot: 1910, *P. comosa* 1 (MNHN A-76), 1906 (*P. comosa*). CROZET ISLANDS: 46°27'S 52°00'E, St. 12, DC 12, *P. comosa*, (MNHN A-921). SOUTH SHETLAND ISLANDS: *Spanish cruise Bentart 94*, coll. *Hespérides*, St. 52, mixed sediment, 62°43'S 60°27'W, 84 m, 1 (MNCNM 1521); St. 71, rocks, 62°43'S 60°26'W, 50 m, 1 (MNCNM 1523); St. 77, mud & organic rests, 62°40'S 60°40'W, 130 m, 1 (MNCNM 1522). TASMAN SEA: 42°17.99'S 170°00.00'E, 958 m depth, 1 (SMF 13225).

Description. Body dorsally arched, ventrally flattened, with well defined intersegmental furrows, segments short (Fig. 66B); all specimens fragmented or lacking posterior end; largest specimen examined (SMNH 3033) 29 mm long, 2.5



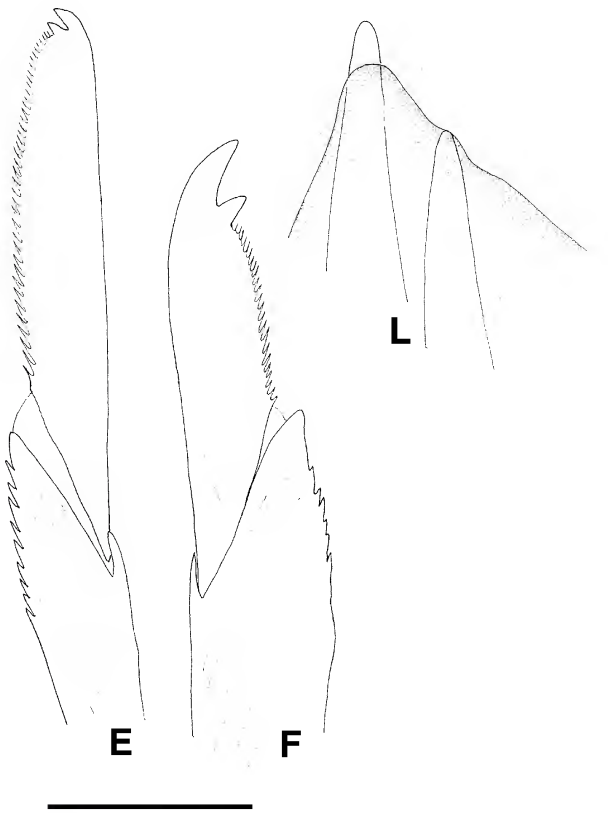


Fig. 67. *Pionosyllis kerguelensis* (McIntosh, 1885) (*A–C*) dorsal, median and ventral compound chaetae, anteriormost parapodium; (*D*) dorsalmost compound chaeta, anterior parapodium; (*E,F*) dorsal and ventral compound chaetae of remaining chaetae, mid-anterior parapodium; (*G*) dorsalmost compound chaeta, mid-posterior parapodium; (*H,I*) dorsal and ventral compound chaetae of remaining chaetae, mid-posterior parapodium; (*J,K*) dorsal and ventral compound chaetae, posterior parapodium; (*L*) aciculae. *A–F*: BMNH 1885.12.1.142; *G–L*: MNHN A-76. Scales: 14 µm.

mm wide for 34 chaetigers; without colour markings (preserved specimens). Prostomium with irregular surface, with longitudinal and transverse grooves forming two posterior cheeks (Fig. 66A,B); 4 eyes arranged in trapezoidal pattern, anterior pair subequal or smaller than posterior one, located on cheeks and often covered by peristomium and chaetiger 1. Palps broad, long, divergent, distally rounded, slightly longer than prostomium, basally fused, with dorsal furrow (Fig. 66A,B). Antennae detached or broken in most specimens; much longer than prostomium (according to Hartman, 1964); median antenna more than twice as long as lateral ones (according to Gravier, 1906), originating just in front of median cleft, lateral antennae inserted on anterior margin of prostomium. Peristomium short, dorsally visible, with 2 pairs of tentacular cirri; dorsal tentacular cirri much longer than ventral ones, similar in shape to antennae and dorsal cirri. Long dorsal cirri smooth basally, weakly crenulated distally, about 4 times as long as body width; short dorsal cirri slightly longer than body width, alternating irregularly with long cirri (Fig. 66B–D). Ventral cirri broad, thick, inflated, almost as large as parapodial lobes on anterior chaetigers (Fig. 66C,D), except those of chaetigers 1–2 (Fig. 66F), shorter and thinner posteriorly (Fig. 66E). Parapodial lobes with long digitiform, dorsal prechaetal papilla (Figs 66C–E). Anterior parapodia with more than 40 compound chaetae, decreasing to about 10 on posterior parapodia. Compound chaetae heterogomph falcigers; shafts increasing in width posteriorly along body and dorsoventrally within fascicle, with spinose endings. Blades bidentate, with short, distally directed spines on margin; with marked dorsoventral and anteroposterior gradation in both shape and size; dorsal blades on anterior and midbody parapodia long, finely spinulated on margin, distal tooth slightly hooked, proximal tooth slightly smaller, ventral blades basally wider, distal tooth hooked and slightly larger than proximal one (Fig. 67A–C); posterior segments with 1–2 dorsal chaetae with elongate, slender blades (Fig. 67D) and remaining chaetae with dorsoventral gradation (Fig. 67E,F); in midbody, this arrangement more marked (Fig. 67G–I); on posterior fascicles, most dorsal chaetae with short blades (Fig. 67J), blades of remaining falcigers similar in length to dorsal ones, but wider, proximal tooth long, triangular (Fig. 67K). Blades of anterior compound chaetae about 100 μm in length dorsally, 40 μm in length ventrally; posterior blades 55 μm in length dorsally, 35 μm in length ventrally. Anterior parapodia with 4–5 straight, thick, aciculae, pointed tip protruding beyond parapodial lobes; posterior parapodia with 1–2 aciculae (Fig. 67L). Dorsal and ventral simple chaetae not seen. Pharynx wide, everted in some specimens, extending through 8–9 chaetigers, with 2 crowns of papillae surrounding opening; pharyngeal tooth conical, located on anterior dorsal rim (Fig. 67A,B). Proventricle barrel shaped, extending to chaetiger 17–18, slightly longer than pharynx.

Habitat. Occurring in fine grey sandy mud, volcanic mud, hard bottom, sand and shells, intertidally to 2916 m (Ehlers, 1913).

Distribution. Coast of North Argentina, Antarctic and Subantarctic seas: Kerguelen Is. South Georgia, Falkland Is., Magellan area, Davis Sea, Palmer Archipelago, Drake Passage, South Orkney Is. Antarctic Peninsula, South Shetland, Australia (Tasmania, New South Wales), New Zealand, Crozet Is.

Pionosyllis koolalya n.sp.

Figs 62A–C, 68A–P, 69A–F

Pionosyllis augeneri.—Hartmann-Schröder, 1991: 359–125. Not Hartmann-Schröder, 1979: 98.

Material examined. HOLOTYPE (AM W28945) AUSTRALIA: SOUTH AUSTRALIA: Speeds Point, Streaky Bay, 32°48'S 134°13'E, coll. P.A. Hutchings, 14 Mar 1979. PARATYPE 1 on SEM stub (AM W28409). NEW SOUTH WALES: Bottle & Glass Rocks, Port Jackson, 33°51'S 151°16'E, substrate unknown, 12m, coll. G. Clark, 11 Dec 1989.

Additional material examined. QUEENSLAND: Heron Is., 23°27'S 151°55'E, sand, intertidal, coll. G. Hartmann-Schröder, id. as *Pionosyllis augeneri* (HMZ P-21018, P-16796).

Description. Holotype 12.8 mm long, 0.3 mm wide, with 71 chaetigers; paratype much smaller. Prostomium oval, with 4 eyes arranged in open trapezoidal pattern (Fig. 68A). Median antenna long, coiled on holotype, several times longer than combined length of prostomium and palps, inserted between posterior eyes; lateral antennae distinctly shorter than median antenna, inserted near anterior margin of prostomium (Figs 68A, 69A–C). Palps broad, similar in length to prostomium or slightly longer. Tentacular and dorsal cirri long, smooth, coiled on holotype, long on anterior segments, becoming shorter on segments beyond proventricle, alternating long cirri (Figs 68C, 69A,B), 2–3 times as long as body width, and short cirri (Fig. 68B), slightly shorter than body width; dorsal cirri with cirrophores. Ciliary bands on dorsum of each segment and areas of dorsal cirri (Fig. 68B–D), distinct on holotype (Fig. 68A); anterior segments with single ciliary band (Fig. 69B,C), double from proventricle segments posteriorly (Fig. 69D). Parapodial lobes conical, ending with 2 lobes (Fig. 68B,D). Ventral cirri digitiform, shorter than parapodial lobes anteriorly, becoming longer posteriorly (Fig. 68B,D). Anterior parapodia with about 10–14 compound chaetae, slightly enlarged, distally truncated shafts, provided with short subdistal spines, and bidentate blades, both teeth similar, with long spines on margin, pointing distally, those of basal part coarse, distal ones thin, reaching or extending beyond proximal tooth, 1–3 slightly longer (Fig. 68E), rest of chaetae within fascicle with slight dorsoventral gradation in length (Fig. 68F), 26 μm in length dorsally, 18 μm in length ventrally. Posteriorly, number of compound chaetae per parapodium decreasing, and blades of 1–3 most dorsal compound chaetae becoming proportionally longer (Figs 68H, 69F) and rest with dorsoventral gradation in length (Figs 68I, 69E); midbody parapodia with 1–2 compound chaetae with relatively long blades, about 31 μm in length, and 4 compound chaetae 15–25 μm in length; proximal tooth proportionally longer than those of anterior chaetae (Fig. 62A). Posterior parapodia with 1 compound chaeta with long blades (Fig. 68K), 33 μm long, and 3 compound chaetae, similar to those of midbody, but with distinctly larger proximal tooth (Figs 68L, 62C), well separated from distal tooth, 18–22 μm in length. Dorsal simple chaetae from midbody, distally bifid to truncate (Figs 68G, 62B), thicker posteriorly, with short, coarse spines on margin (Fig. 68 O). Ventral simple chaetae on posterior parapodia, sigmoid, thick, strongly bidentate, both teeth well separated, almost at 90°, proximal tooth long, broad, slightly hooked, with few, long subdistal spines, surpassing level of proximal tooth (Figs 68P, 62C). Two aciculae on anterior segments (Fig. 68M), 1 from proventricle segments onwards, distally bilobed (Fig. 68J), thicker on posterior parapodia (Fig. 68N). Pharynx through

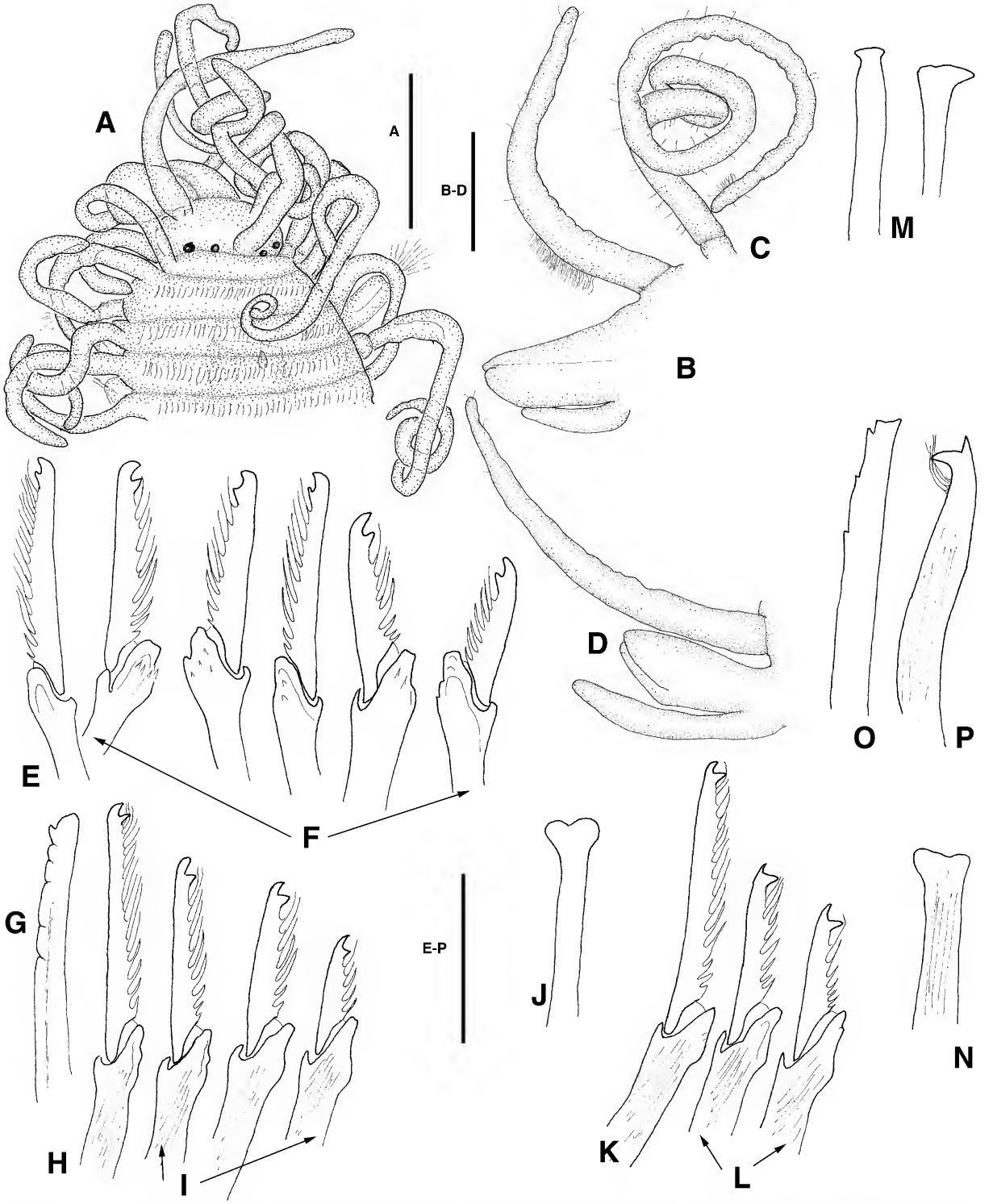


Fig. 68. *Pionosyllis koolalya* n.sp. (*A*) anterior end, dorsal view; (*B*) midbody parapodium with short dorsal cirri; (*C*) long dorsal cirri, midbody; (*D*) posterior parapodium; (*E*) long-bladed compound chaeta, anterior parapodium; (*F*) compound chaetae, anterior parapodium; (*G*) dorsal simple chaeta, midbody; (*H*) long-bladed compound chaeta, midbody; (*I*) compound chaetae, midbody; (*J*) acicula, midbody; (*K*) long-bladed compound chaeta, posterior parapodium; (*L*) dorsal and ventral compound chaetae, posterior parapodium; (*M*) aciculae, anterior parapodium; (*N*) acicula, posterior parapodium; (*O*) dorsal simple chaeta, posterior parapodium; (*P*) ventral simple chaeta. AM W28409. Scales: *A* 0.18 mm, *B–D* 97 μm, *E–P* 20 μm.

about 6 segments, pharyngeal tooth located on anterior rim. Proventricle through 4 segments, with about 26 muscle cell rows. Pygidium small, with 2 anal cirri.

Remarks. *Pionosyllis koolalya* is similar to *P. serrata* described above but differs mainly in lacking enlarged anterior parapodia with thick compound chaetae with markedly short blades; remaining compound chaetae are rather similar, but the dorsal simple chaeta of *P. koolalya* is truncated, and slightly bifid in *P. serrata*. All other species of the genus are provided with long, spiniger-like chaetae. These two species also have fewer compound chaetae with

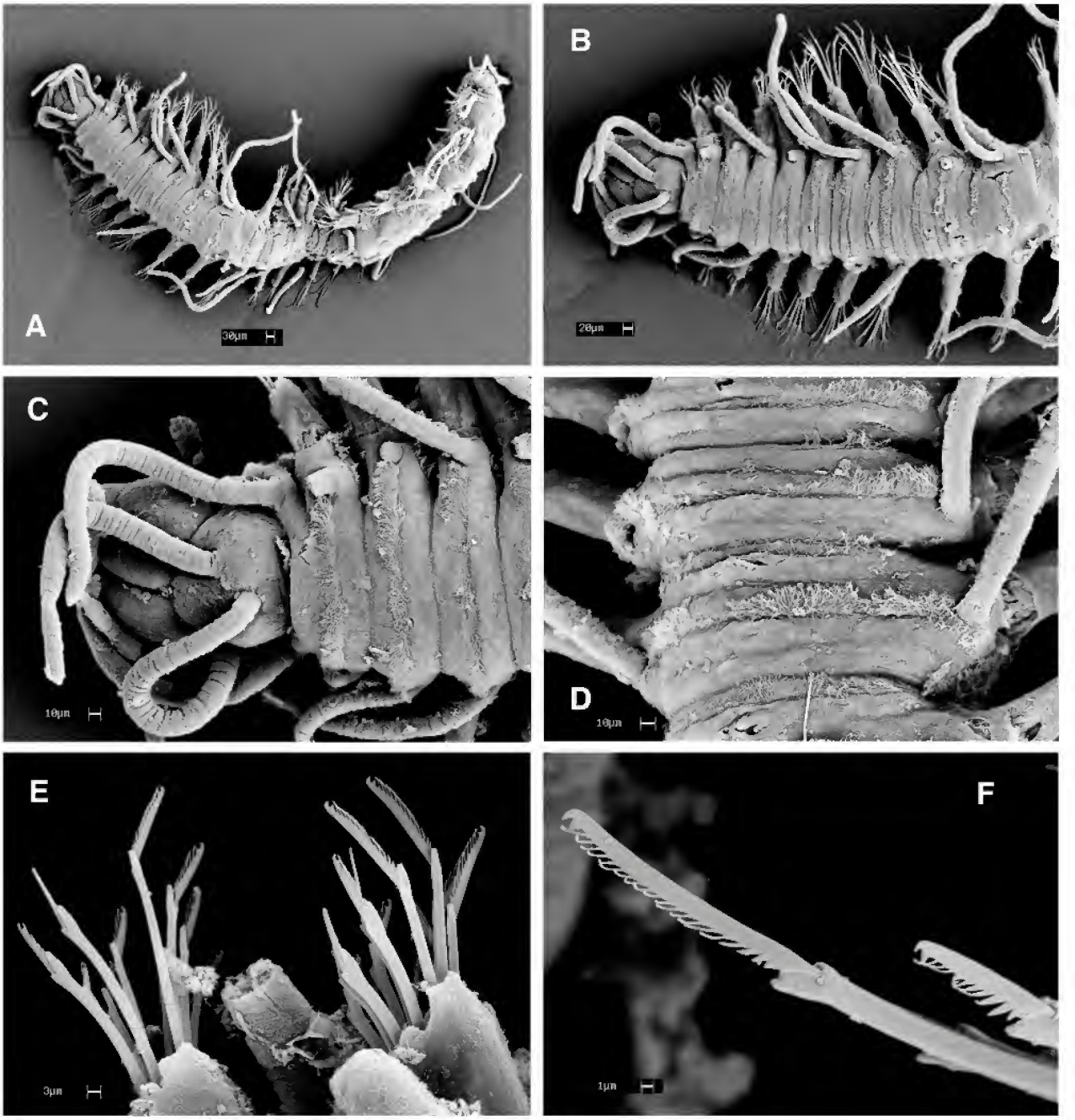


Fig. 69. SEM of *Pionosyllis koolalya* n.sp. (*A*) incomplete specimen, dorsal view; (*B*) anterior end, dorsal view; (*C*) detail of same; (*D*) detail of dorsum, midbody; (*E*) compound chaetae, midbody; (*F*) long-bladed compound chaeta, and one short-bladed, compound chaeta. Paratype, AM W28409.

distinctly longer blades than other chaetae in the fascicle, but they are relatively short and less than half the length of the longest bladed chaetae. Some material of *P. augeneri* (Hartmann-Schröder, 1991) from Heron Island, Queensland, belong to this new species.

Habitat. Unknown, occurring from intertidal to 12 m.

Distribution. Australia (South Australia, New South Wales, Queensland).

Etymology. The specific name comes from an aboriginal word, *koolalya*, meaning feather epaulettes, in reference to the ciliated dorsum.

Pionosyllis mariae n.sp.

Figs 46D–F, 70A–J, 71A–F, 72A–C

Material examined. HOLOTYPE (AM W28454) AUSTRALIA: QUEENSLAND: Outer Yonge Reef, Great Barrier Reef, 14°36'S 145°38'E, rock with *Lithothamnion* & *Halimeda*, 30 m, coll. P.A. Hutchings, 24 Jan 1977. PARATYPE (AM W28921) Outer Yonge Reef, Great Barrier Reef, 14°36'S 145°38'E, rock covered with pink coralline algae, encrusting sponges, 9 m, coll. P.A. Hutchings, 21 Jan 1977.

Other material examined. NEW SOUTH WALES: Taupo Seamount, Tasman Sea, 33°16.85'S 156°09.15'E, limestone & sand bottom, 244 m, coll. J.K. Lowry & party on RV *Franklin*, 2 May 1989, 1 on SEM stub (AM W28873).

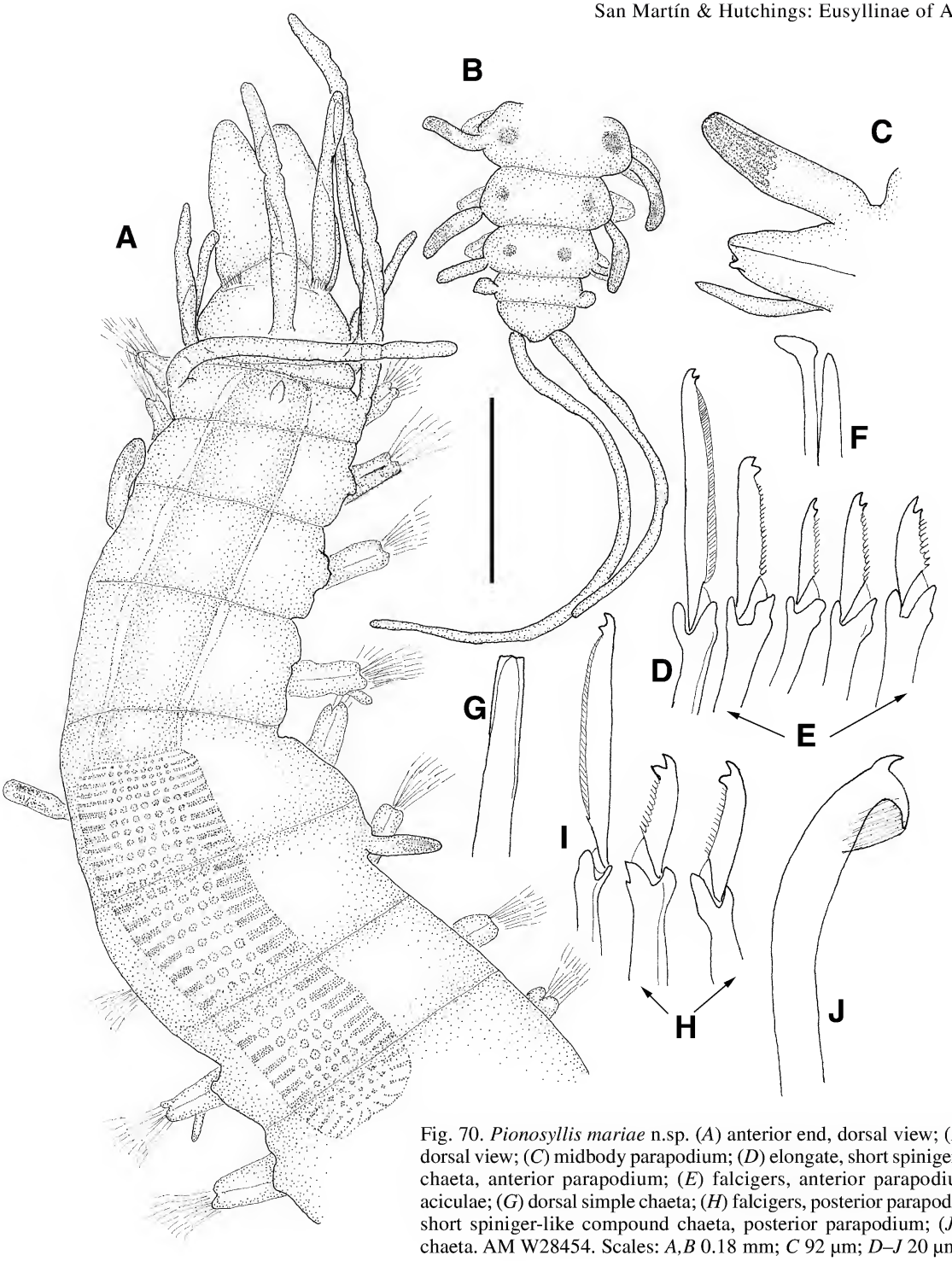


Fig. 70. *Pionosyllis mariae* n.sp. (*A*) anterior end, dorsal view; (*B*) posterior end, dorsal view; (*C*) midbody parapodium; (*D*) elongate, short spiniger-like, compound chaeta, anterior parapodium; (*E*) falcigers, anterior parapodium; (*F*) anterior aciculae; (*G*) dorsal simple chaeta; (*H*) falcigers, posterior parapodium; (*I*) elongate, short spiniger-like compound chaeta, posterior parapodium; (*J*) ventral simple chaeta. AM W28454. Scales: *A,B* 0.18 mm; *C* 92 μm; *D–J* 20 μm.

Description. Body slender, filiform (Fig. 46D), 7 mm long, 0.3 mm wide, 54 chaetigers. Prostomium pentagonal to triangular, with 4 eyes in open trapezoidal arrangement, and sometimes 2 anterior eyespots. After fixation, however, eyes may be absent (Fig. 70A). Lateral antennae inserted between anterior eyes and eyespots, near anterior margin of prostomium, smooth, similar in length to palps; median antenna arising between posterior eyes, long, often curled, distally pseudoarticulated, broken on holotype (Fig. 70A), more than twice length of prostomium. Palps longer than prostomium, triangular, directed behind, fused basally. Two transverse, small, ciliated furrows on prostomium (Figs 46F arrow, 70A). Peristomium distinct, slightly shorter than subsequent segments; tentacular cirri elongated, dorsal tentacular cirri longer than lateral antennae, shorter than median one, ventral tentacular cirri shorter than dorsal ones (Figs 46E,F, 70A). Dorsal cirri of chaetiger 1 long, slender, similar to median antenna, sometimes pseudoarticulated distally. Dorsal cirri short, slightly longer than parapodial lobes, fusiform (Fig. 71A,B), distally more or less truncated (Fig. 70A,C), usually with some fibrillar inclusions, with terminal pore (Fig. 71C arrow). Dorsal cirri absent on chaetiger 2, tuft of cilia present (Fig. 46E,F arrow). Parapodia conical, with distal papilla (Figs 70C, 71A).

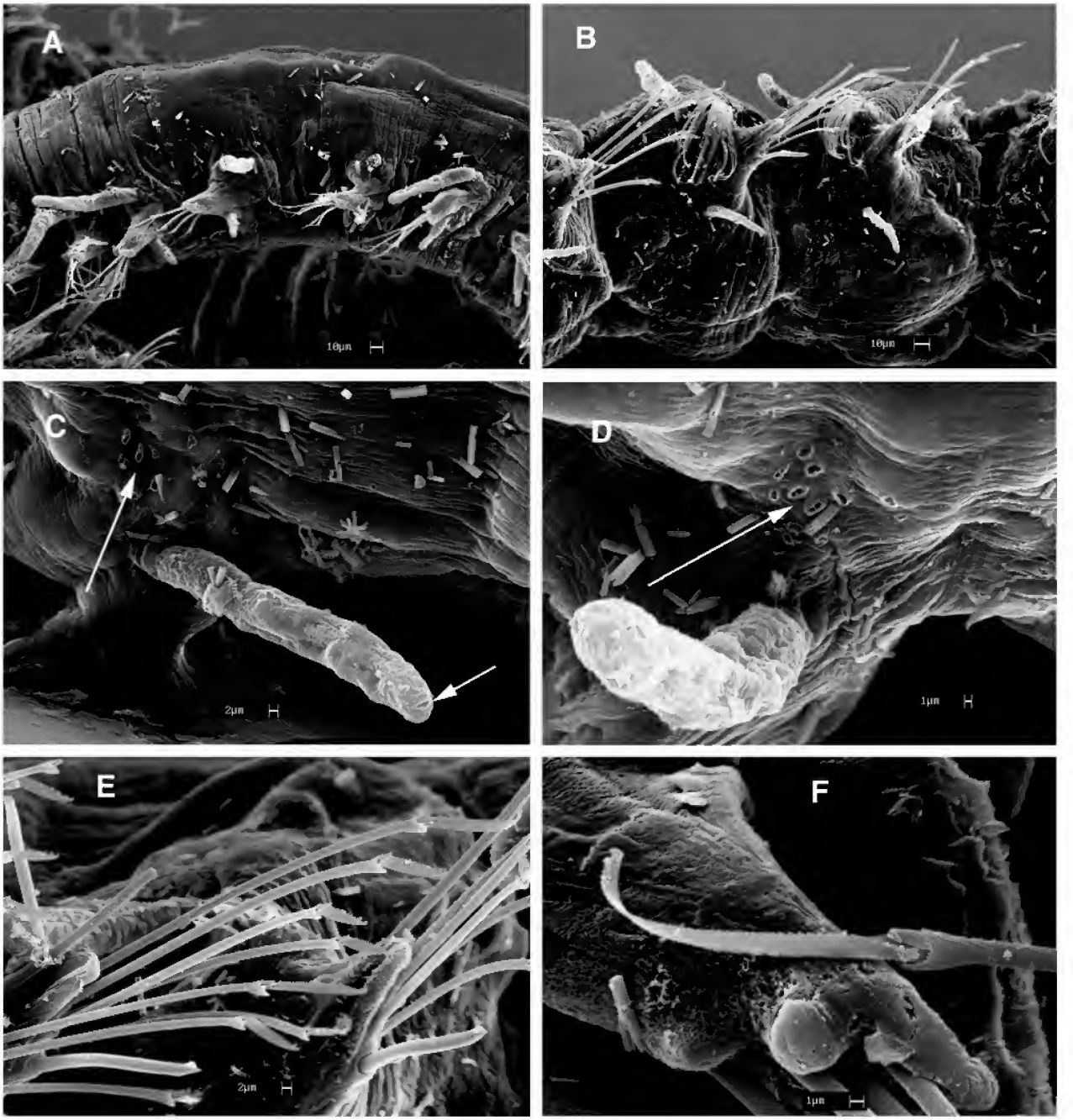


Fig. 71. SEM of *Pionosyllis mariae* n.sp. (*A*) midbody, lateral view; (*B*) the same of an epigamic specimen, showing the capillary notochaetae; (*C*) dorsal pores and distal pore of dorsal cirrus (arrows); (*D*) detail of dorsal pores (arrow); (*E*) chaetal fascicle, mid-posterior parapodium; (*F*) short, spiniger-like chaeta. AM W28873.

Ventral cirri digitiform, slender, slightly longer than parapodial lobes on posterior parapodia. Compound chaetae with hemigomph articulation, smooth distally on shafts; blades of 2 kinds, most dorsal chaetae with elongated, short spiniger-like, bidentate blades, spines on margin apparently jointed by membrane (Figs 70D,I, 71F), remaining chaetae with short, bidentate blades, with short spines on margin (Figs 70E, 71E), more strongly bidentate on posterior parapodia (Figs 70H, 72A). Anterior parapodia each with 1 compound chaetae with elongated blade, about 27 µm in length, and 4 chaetae with shorter blades, 17–12 µm in length; posterior parapodia with 1 compound chaetae with elongate blade and 2–3 short-bladed, all similar in size to anterior ones. Dorsal simple chaetae from midbody, smooth, distally truncate (Fig. 72B), with small, indistinct hood (Fig. 70G). Ventral simple chaetae from mid-posterior parapodia, large, acicular, prominent, with subdistal translucent hood, bidentate, proximal tooth long, hooked, distal tooth smaller, also hooked (Figs 70J, 71E, 72C). Anterior parapodia each with 2 aciculae, one straight, other bent at tip (Fig. 70F); solitary acicula on remaining parapodia, bent tip, thicker than anterior ones. Dark glands on each parapodia from midbody (Fig. 70B) with dorsal pores (Fig. 71C,D arrows). Pharynx through about 4 segments; pharyngeal tooth anteriorly located (Fig. 70A). Proventricle rectangular, through 3–4 segments, with 30–36 muscle cell rows.

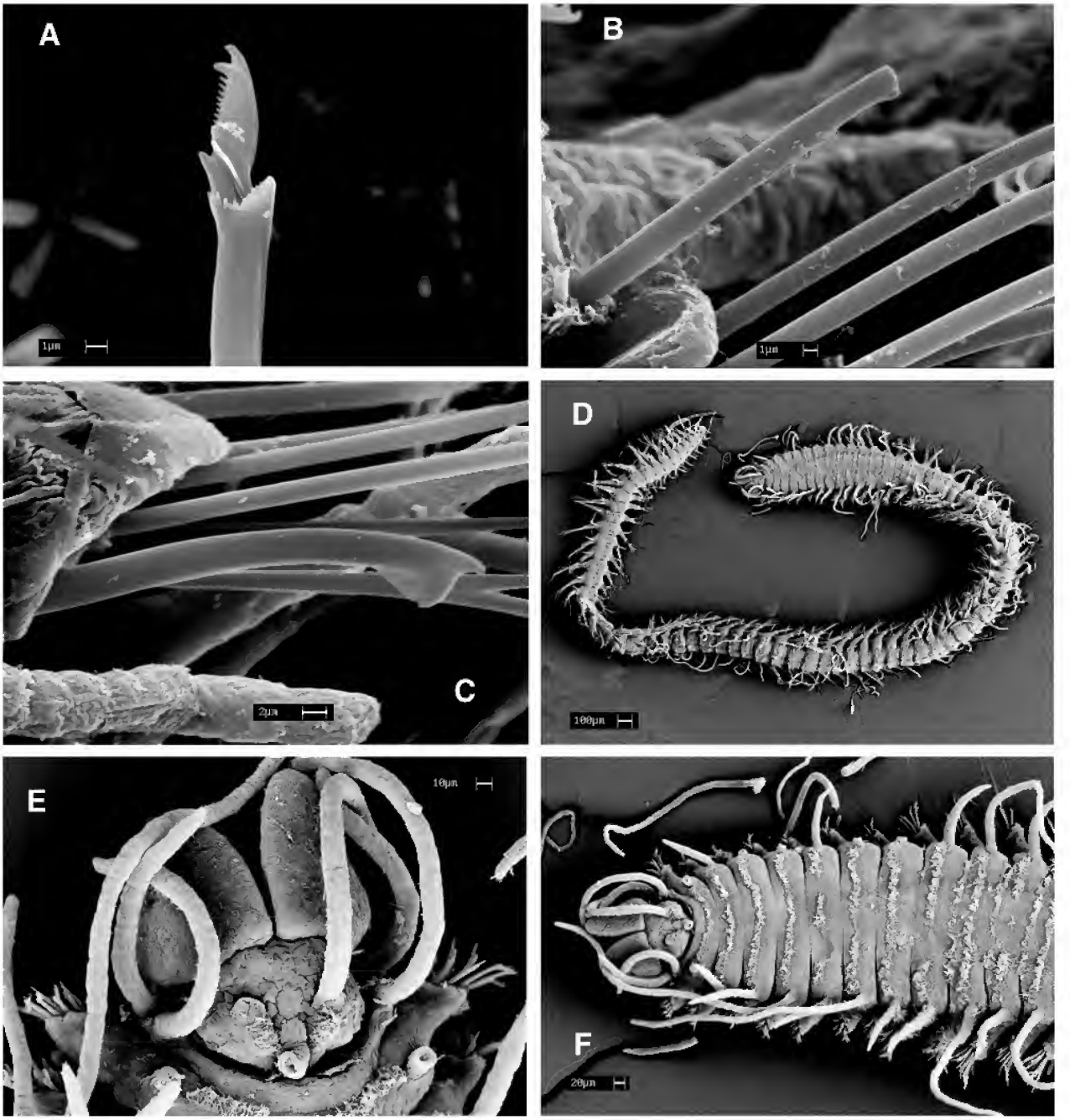


Fig. 72. SEM of *Pionosyllis mariae* n.sp. (*A*) falciger, posterior parapodium; (*B*) dorsal simple chaeta; (*C*) ventral simple chaeta. SEM of *Pionosyllis serrata* (Hartmann-Schröder, 1984) (*D*) complete specimen, dorsal view; (*E*) prostomium and palps, dorsal view; (*F*) anterior end, dorsal view. *A–C*: AM W28873, *D–F*: AM W28913.

Pygidium semi-circular, with 2 long, slender anal cirri (Fig. 70B), similar in length to median antenna. Mature specimen with notoacicula and natatory chaetae from chaetiger 17. One specimen epigamic, with natatory chaetae on midbody and posterior segments (Fig. 71B).

Remarks. *Pionosyllis mariae* n.sp. is similar to *P. weismanni* Langerhans, 1879, a worldwide reported species, that probably represents a complex of morphologically similar species (San Martín, 2003), since small differences among specimens from different parts of the world have been reported (see Ben-Eliahu, 1977). The Australian specimens are distinctly smaller than those of the Mediterranean Sea (7 mm versus 18 mm) and lack dorsal cirri on chaetiger 2, which are always present on Mediterranean specimens (see San Martín, 2003).

Habitat. Occurring as cryptic species in encrusting communities and in sand, in depths of 9 to 244 m.

Distribution. Australia (Queensland, New South Wales).

Etymology. The new species is named after María Capa, collaborator and friend.

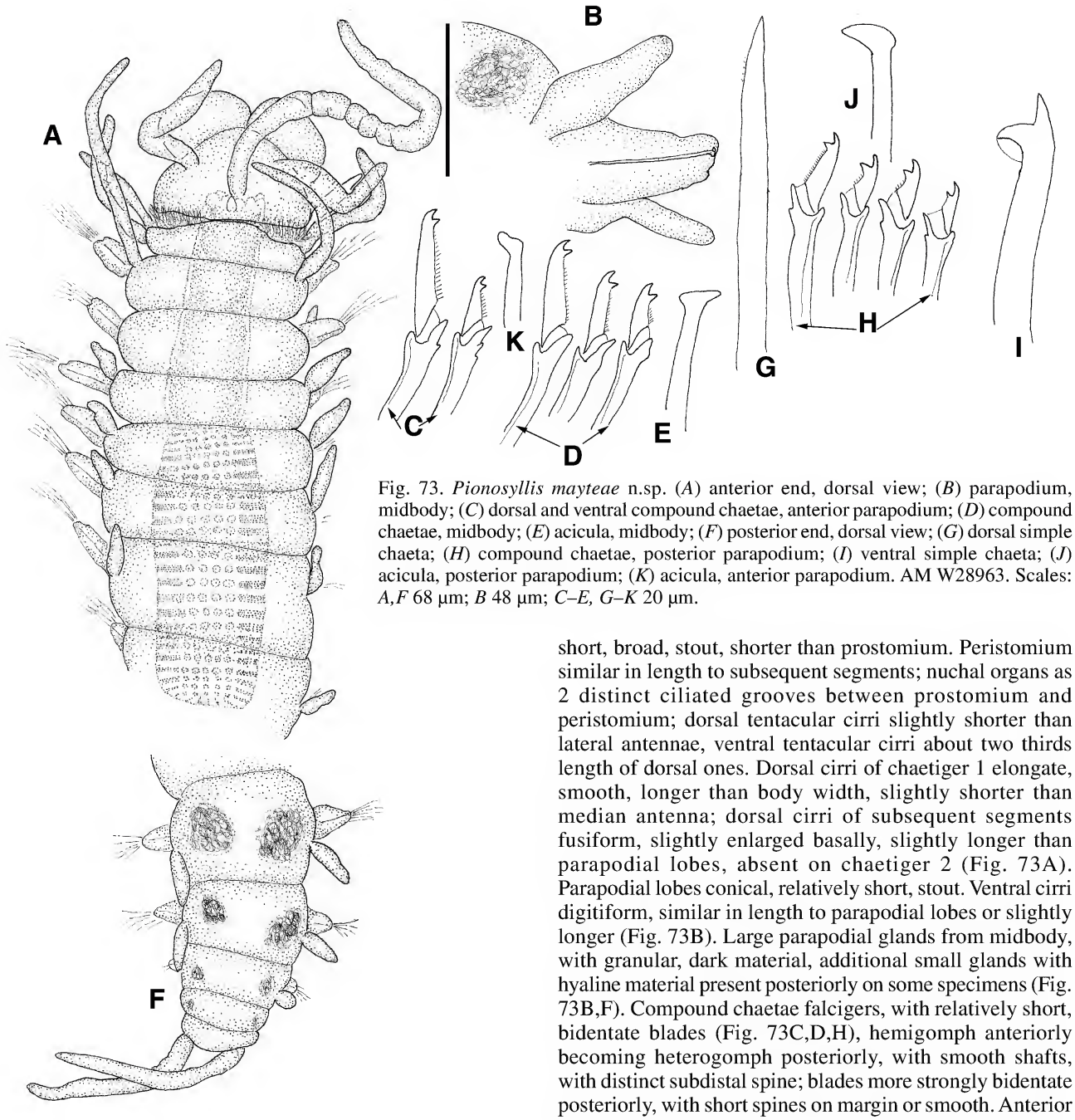


Fig. 73. *Pionosyllis mayteae* n.sp. (*A*) anterior end, dorsal view; (*B*) parapodium, midbody; (*C*) dorsal and ventral compound chaetae, anterior parapodium; (*D*) compound chaetae, midbody; (*E*) acicula, midbody; (*F*) posterior end, dorsal view; (*G*) dorsal simple chaeta; (*H*) compound chaetae, posterior parapodium; (*I*) ventral simple chaeta; (*J*) acicula, posterior parapodium; (*K*) acicula, anterior parapodium. AM W28963. Scales: *A,F* 68 µm; *B* 48 µm; *C–E, G–K* 20 µm.

***Pionosyllis mayteae* n.sp.**

Fig. 73A–K

Material examined. HOLOTYPE (AM W29245) AUSTRALIA: QUEENSLAND: Outer Yonge Reef, Great Barrier Reef, 14°36'S 145°38'E, rock with *Lithothamnion* & *Halimeda*, 30 m, coll. P.A. Hutchings, 24 Jan 1977. PARATYPES 5 (AM W28963) Outer Yonge Reef, Great Barrier Reef, 14°36'S 145°38'E, rock with *Lithothamnion* & *Halimeda*, 30 m, coll. P.A. Hutchings, 24 Jan 1977.

Description. Body slender, less filiform than other species of the genus above described, 5.4 mm long, 0.2 mm wide, with 44 chaetigers. Prostomium semi-circular to pentagonal, apparently without eyes. Median antenna elongate, about twice combined length of prostomium and palps, rugose to indistinctly articulated, inserted near posterior margin of prostomium; lateral antennae smooth, about half length of median antenna, arising laterally in front (Fig. 73A). Palps short, broad, stout, shorter than prostomium. Peristomium similar in length to subsequent segments; nuchal organs as 2 distinct ciliated grooves between prostomium and peristomium; dorsal tentacular cirri slightly shorter than lateral antennae, ventral tentacular cirri about two thirds length of dorsal ones. Dorsal cirri of chaetiger 1 elongate, smooth, longer than body width, slightly shorter than median antenna; dorsal cirri of subsequent segments fusiform, slightly enlarged basally, slightly longer than parapodial lobes, absent on chaetiger 2 (Fig. 73A). Parapodial lobes conical, relatively short, stout. Ventral cirri digitiform, similar in length to parapodial lobes or slightly longer (Fig. 73B). Large parapodial glands from midbody, with granular, dark material, additional small glands with hyaline material present posteriorly on some specimens (Fig. 73B,F). Compound chaetae falcigers, with relatively short, bidentate blades (Fig. 73C,D,H), hemigomph anteriorly becoming heterogomph posteriorly, with smooth shafts, with distinct subdistal spine; blades more strongly bidentate posteriorly, with short spines on margin or smooth. Anterior and midbody parapodia with 5 compound chaetae, blades 16 µm in length dorsally, 8 µm in length ventrally; 4 compound chaetae on each posterior parapodia, blades 7–10 µm in length. Dorsal simple chaetae from mid-posterior segments, long, straight, acute, distally pointed, with minute subdistal spines on margin (Fig. 73G). Ventral simple chaetae on posterior parapodia, thick, strongly bidentate, teeth at 90°, proximal tooth slightly hooked, with small translucent hood (Fig. 73I). Acicula solitary throughout, slender, slightly larger posteriorly, distally expanded laterally with convex surface (Fig. 73E,J). Pygidium semi-circular, with 2 long anal cirri, smooth, similar in length to dorsal cirri of chaetiger 1 (Fig. 73F). Pharynx through 5 segments; pharyngeal tooth on anterior rim (Fig. 73A). Proventricle through 5 segments, with 20 muscle cell rows.

Remarks. *Pionosyllis mayteae* n.sp. differs from similar other species of the genus in lacking compound chaetae

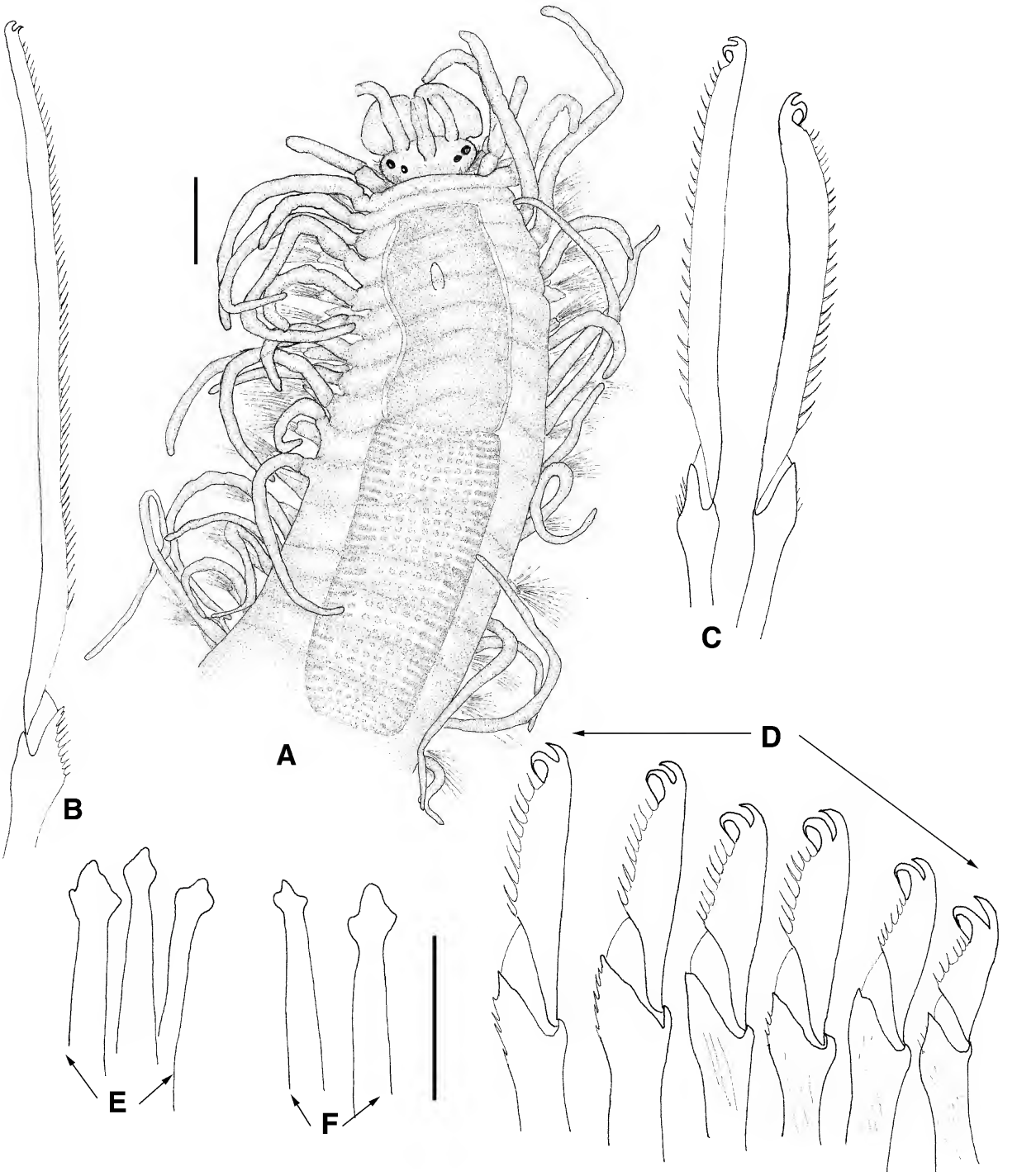


Fig. 74. *Pionosyllis rousei* n.sp. (*A*) anterior end, dorsal view; (*B*) spiniger-like compound chaeta, anterior parapodium; (*C*) spiniger-like compound chaetae, midbody; (*D*) falcigers, midbody; (*E*) aciculae, anterior parapodium; (*F*) aciculae, midbody. AM W28840 (holotype). Scales: *A* 0.18 mm; *B–F* 20 μm.

with elongated blades and having distally pointed dorsal simple chaetae; and ventral simple chaetae bidentate with teeth at 90°.

Habitat. Occurring on encrusting *Lithothamnion* and *Halimeda* at depths of 30 m.

Distribution. Australia (Queensland).

Etymology. The species is named after María Teresa Aguado (Mayte), collaborator and friend.

Pionosyllis rousei n.sp.

Fig. 74A–F

Material examined. HOLOTYPE (AM W29230), TASMAN SEA: reef flat near *Yoshin Maru Iwaki* wreck, Elisabeth Reef, 29°55.48'S 159°01.18'E, Elisabeth & Middleton Reefs Expedition, St. 43, 14 Dec 1987. PARATYPES 4 (AM W28840), reef flat near *Yoshin Maru Iwaki* wreck, Elisabeth Reef, TASMAN SEA, 29°55.48'S 159°01.18'E, Elisabeth & Middleton Reefs Expedition, St. 43, 14 Dec 1987.

Additional material examined. TASMAN SEA: Taupo Seamount, 33°16.51'S 156°09.09'E, limestone & sand bottom, 244 m, coll. J.K. Lowry, on RV Franklin, 2 May 1989, 3 (AM W28836).

Description. Holotype best preserved individual, incomplete specimen, 2.2 mm long, 0.6 mm wide, with 22 chaetigers. Body fragile, dorsally arched, cylindrical, without colour pattern, yellowish in alcohol. Prostomium oval, with 4 eyes in open trapezoidal arrangement. Antennae damaged; lateral antennae inserted near anterior margin of prostomium, median antenna inserted on middle of prostomium. Palps large, slightly longer than prostomium, free from each other (Fig. 74A). Nuchal organs ciliated, extending to lateral margins of prostomium (Fig. 74A). Peristomium dorsally reduced, covered by chaetiger 1. Anteriormost segments short, becoming longer from proventricle onwards. Left dorsal tentacular cirrus missing, right one appears broken; ventral tentacular cirri shorter than dorsal cirri. Dorsal cirri smooth, with distinct cirrophores, elongated, alternating irregularly long and short (Fig. 74A), long cirri similar in length to body width, shorter cirri less than half length of longer ones. Parapodial lobes conical. Ventral cirri elongated, similar in length to parapodial lobes. Compound chaetae heterogomph, blades of two kinds, spiniger-like and falcigers. Midbody parapodia with 2 spiniger-like chaetae, with short spines on margin, distinctly bidentate, distal tooth hooked, and proximal tooth curved, with tendon contacting with margin, about 40–35 µm long (Fig. 74C), and 8–11 falcigers, strongly bidentate, long and hooked distal tooth and long, curved proximal tooth, provided with distinct tendon contacting with edge of blade, slight dorsoventral gradation in length of blades within fascicle, 25 µm dorsally and 15 µm ventrally (Fig. 74D), with thin spines on margin. Anteriormost parapodia with 1–2 distinctly long, slender, spiniger-like chaetae present, blades about 86 µm in length, bidentate, with both blades similar in size, proximal tooth slightly recurved, but without tendon (Fig. 74B). Dorsal and ventral simple chaetae not seen. Aciculae tricuspid, 3 on anterior parapodia (Fig. 74E), 2 on midbody parapodia (Fig. 74F). Pharynx wide, though about 7–8 segments; pharyngeal tooth conical, located in front of middle of pharynx (Fig. 74A). Proventricle through 7 segments, similar in size to pharynx, with about 28 muscle cell rows.

Remarks. *Pionosyllis rousei* n.sp. is characterized by having compound chaetae distinctly bidentate, with both teeth similar and well separated from each other. *Pionosyllis serratisetosa* (López, San Martín & Jiménez, 1997), from southwestern Mediterranean has similar chaetae, but the teeth on the blades are not separated and are smaller, the blades have a different shape; long spiniger-like compound chaetae are absent, and the pharyngeal tooth is located near anterior margin of pharynx. *Pionosyllis longocirrata* (Saint-Joseph, 1887), from the eastern Atlantic and Mediterranean Sea, also has the pharyngeal tooth located more anteriorly than *P. rousei*, and the blades of compound chaetae either have a minute distal tooth or none (see San Martín, 2003, for more details). *Pionosyllis templadoi* (San Martín, 1991) from Cuba has a similar body and the position of pharyngeal tooth is also similar. The blades of compound chaetae, however, have a small distal tooth and an elongated proximal tooth (San Martín, 1991). *Pionosyllis luquei* (San Martín, 1990), also from Cuba, has similar compound chaetae, although not as strongly hooked, with well-developed teeth, but the dorsal cirri are shorter, and the pharyngeal tooth is located more posteriorly (San Martín, 1990).

Habitat. Substrate unknown, recorded from 244 m depth.

Distribution. Tasman Sea (Elisabeth and Middleton Reef).

Etymology. This species is named after Dr Greg Rouse, an Australian Polychaetologist.

Pionosyllis serrata (Hartmann-Schröder, 1984)

Figs 72D–F, 75A–N, 76A–F, 77A–F

Eusyllis serrata Hartmann-Schröder, 1984: 18, figs 23–26.

Material examined. AUSTRALIA: NEW SOUTH WALES: East of Bondi, 33°53.1'S 151°17.4'E, sand, 30 m, Fisheries Research Institute, 24 July 1989, 2 (AM W24373); Bass Point, 34°36'S 150°54'E, 50 m, coll. The Ecology Lab, Ready Mixed Industries, 1 Feb 1990, 3 (AM W28922); Bass Point, 34°36'S 150°54'E, 50 m, coll. The Ecology Lab, Ready Mixed Industries, 1 Feb 1990, 2 on SEM stub (AM W28913).

Description. Body fragile (Fig. 72D), 8.7 mm long, 0.4 mm wide, with 77 chaetigers, pale in alcohol. Prostomium oval, slightly wider than long, with 4 eyes in open trapezoidal arrangement (Fig. 75A); median antenna more than twice as long as prostomium and palps together, inserted between posterior eyes, near posterior margin of prostomium; lateral antennae shorter than median antenna, similar or slightly longer than combined length of prostomium and palps, inserted near anterior margin; two tufts of cilia posterior to insertion of lateral antennae (Fig. 72E). Palps long and basally broad, triangular, longer than prostomium (Figs 72E, 75A), free for almost entire length, basally fused. Peristomium dorsally reduced. Anterior segments with single transverse row of cilia (Figs 72F, 75A); midbody and posterior segments each with double row of cilia (Fig. 76A,B). Antennae, tentacular and dorsal cirri long, slender, filiform, smooth, sometimes coiled, of 2 sizes, long and short, long ones distinctly longer than body width, short ones similar in length to half of body width (Figs 72D,F, 75A, 76A,B). Dorsal tentacular cirri long, ventral ones short. Parapodia of anterior 8–10 chaetigers enlarged, wide, distally truncated (Fig. 75A) with several small, rounded lobes distally (Fig. 75M), and numerous, about 12–14 short, broad compound chaetae, with enlarged shafts and short, bidentate blades (Fig. 76D), about 22–16 µm in length, with few, long, thick spines on margin, distal ones extending beyond proximal tooth (Figs 75B, 76E). Posterior to proventricle, parapodial lobes becoming conical, slender, with terminal papilla; compound chaetae from proventricle parapodia without enlarged shafts, apparently smooth and distally truncated, and elongated blades with long, thin spines on margin, distally ornamented, distal ones slightly longer than others, extending beyond proximal tooth and sometimes reaching level of distal tooth; most dorsal compound chaetae with more elongate, bidentate blades (Figs 75C,F,I, 76F, 77A), about 40 µm in length on post-proventricle segments, 35 µm on midbody parapodia, 42 µm on posterior parapodia, and several compound chaetae with shorter blades, and dorsoventral gradation in length within fascicle (Figs 75D,G,J,K, 76F, 77B,C), 13–26 µm on proventricle segments, 16–25 µm on midbody parapodia, 16–37 µm on posterior parapodia; compound chaetae 8–10

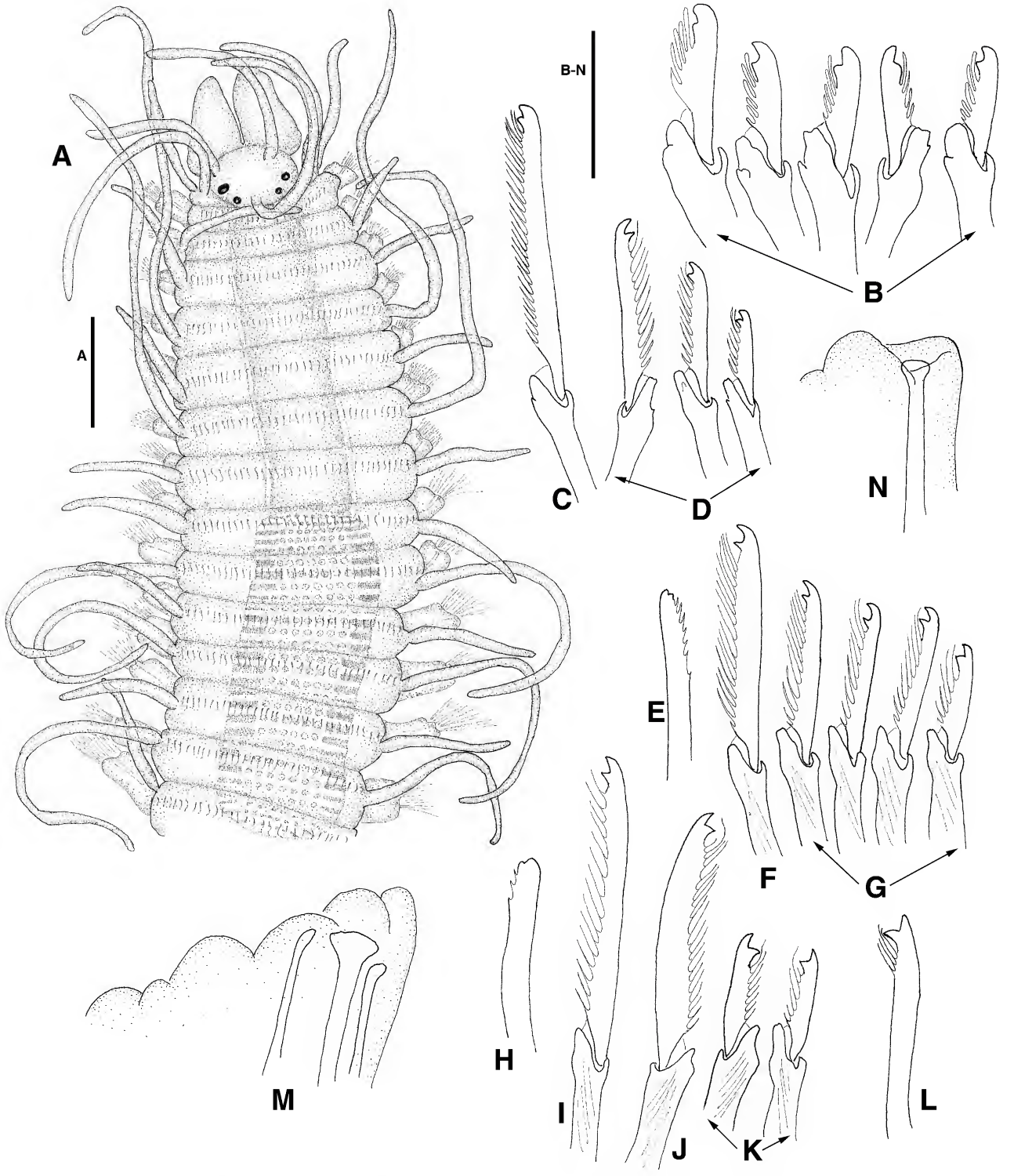


Fig. 75. *Pionosyllis serrata* (Hartmann-Schröder, 1984); (*A*) anterior end, dorsal view; (*B*) compound chaetae, anteriormost parapodium; (*C*) dorsalmost compound chaeta, anterior parapodium; (*D*) compound chaetae, anterior parapodium; (*E*) dorsal simple chaeta, midbody; (*F*) dorsalmost compound chaeta, midbody; (*G*) compound chaetae, midbody; (*H*) dorsal simple chaeta, posterior parapodium; (*I*) dorsalmost compound chaeta, posterior parapodium; (*J,K*) compound chaetae, posterior parapodium; (*L*) ventral simple chaeta; (*M*) aciculae and edge of anteriormost parapodium; (*N*) acicula and edge of posterior parapodium. AM W28922. Scales: *A* 0.18 mm, *B–N* 20 µm.

on proventricle segments, about 7 on midbody, 4 on posterior parapodia. Blades of posterior chaetae markedly bidentate, both teeth well separated, almost at 90°, and slightly convex (Figs 75J,K, 77D). Dorsal simple chaetae from midbody, distally weakly bifid (Fig. 75E), with some spines on margin, becoming thicker posteriorly, with shorter spines on margin (Figs 75H, 77E). Ventral simple chaetae on posterior parapodia, thick, strongly bidentate, both teeth almost at 90°, proximal tooth slightly hooked, and few, long spines on margin, extending beyond proximal tooth (Figs

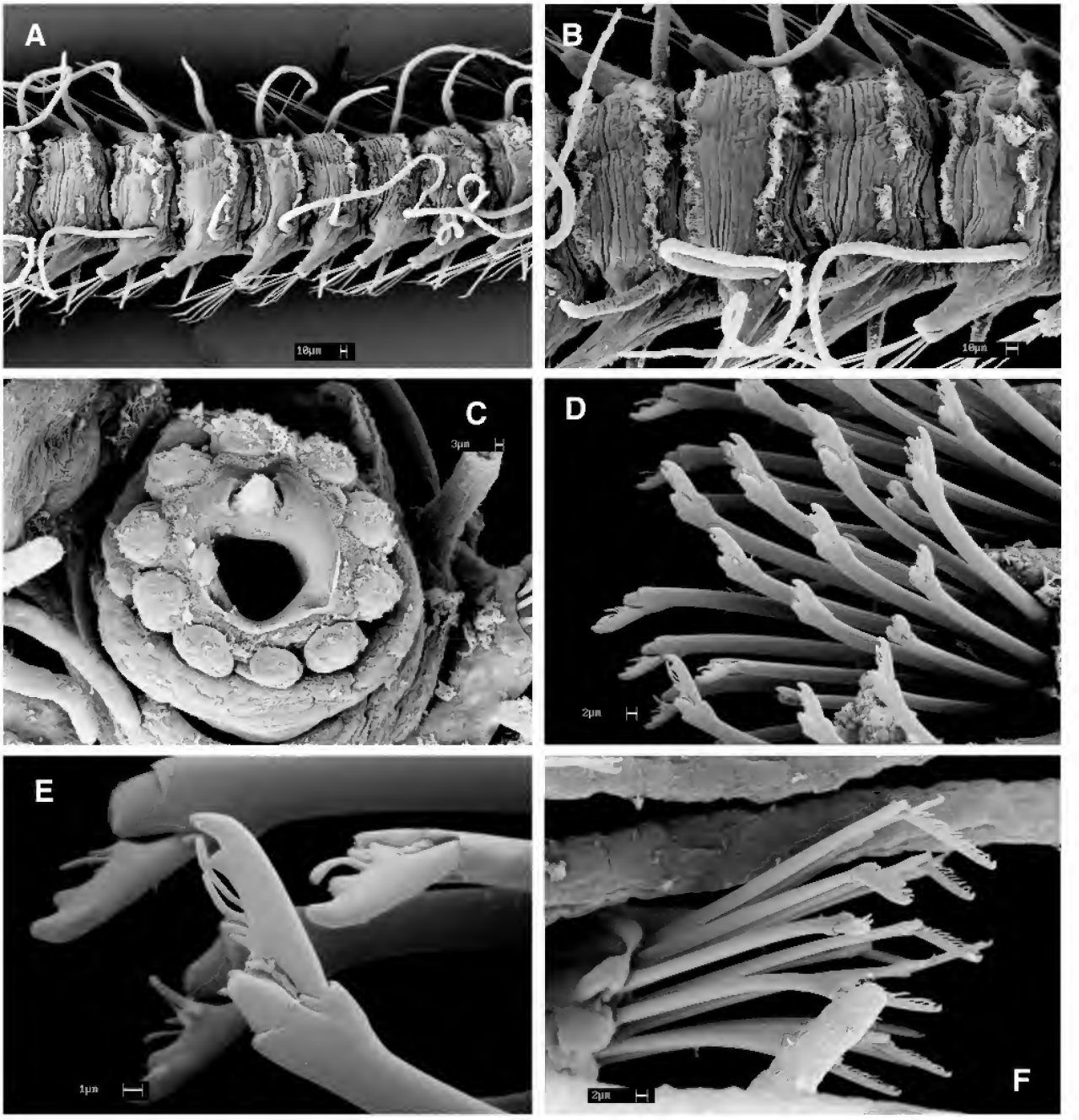


Fig. 76. SEM of *Pionosyllis serrata* (Hartmann-Schröder, 1984) (*A*) midbody, dorsal view; (*B*) detail of the same; (*C*) everted pharynx; (*D*) anteriormost compound chaetae; (*E*) compound chaeta, anteriormost parapodium; (*F*) compound chaetae, midbody. AM W28913.

75L, 77F). Aciculae distally knobbed, 3 on anterior parapodia (Fig. 75M), diminishing progressively along body to 1 (Fig. 75N). Pharynx through about 6–7 segments; pharyngeal tooth located anteriorly, surrounded by crown of 10 soft papillae and layer of cilia (Fig. 76C). Proventricle through 7 segments, with 30 muscle cell rows. Two long, filiform anal cirri (Fig. 72D).

Habitat. Occurring in sandy substrates, from intertidal to about 30 m.

Distribution. Australia (Western Australia, New South Wales).

Pionosyllis yolandae n.sp.

Figs 42C–F, 49A–C, 78A–J

Material examined. HOLOTYPE (AM W28222) AUSTRALIA: NEW SOUTH WALES: Burrill Rocks, 35°23.39'S 150°28.24'E, on gorgonacean, 24 m, coll. R.T. Springthorpe, 7 May 1997. PARATYPES 1 (AM W28401) S ledge, Cook Is., 28°11.65'S 153°34.63'E, colonial ascidian, 14 m, coll. G.D.F. Wilson, 9 Jun 1993; 1 (AM W28964) N side of Bannister Head, N of Ulladulla, 35°19.15'S 150°29.12'E, grey sponge from top of boulder, 18 m, K. Attwood, 6 May 1997.

Other material examined. TASMAN SEA Taupo Seamount, 33°16.85'S 156°09.15'E, limestone & sand bottom, 244 m, coll. J.K. Lowry & party, on RV *Franklin*, 2 May 1989, 3 on SEM stub (AM W28876); Taupo Seamount, 33°16.85'S 156°09.15'E, limestone & sand

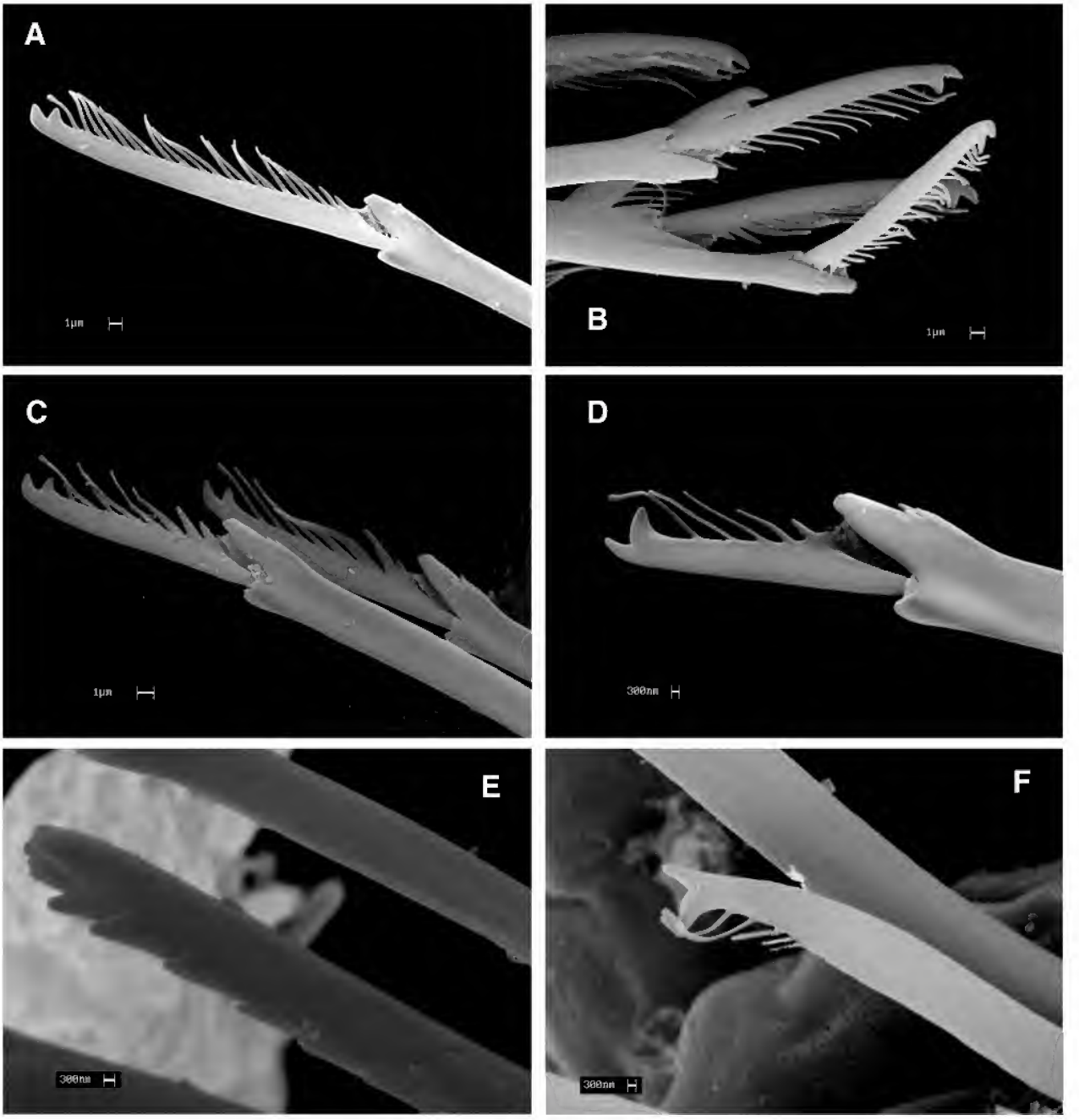


Fig. 77. SEM of *Pionosyllis serrata* (Hartmann-Schröder, 1984) (*A*) dorsalmost compound chaeta, midbody; (*B,C*) dorsal and ventral compound chaetae, midbody; (*D*) ventral compound chaeta, posterior parapodium; (*E*) dorsal simple chaeta; (*F*) ventral simple chaeta. AM W28913.

bottom, 244 m, coll. J.K. Lowry & party, on RV *Franklin*, 2 May 1989, few (AM W28924). WESTERN AUSTRALIA: Reef W of groyne, 2 km S of Cape Peron, 32°16'S 115°41'E, orange sponge in deep channel in limestone reef, 4.5 m, coll. R.T. Springthorpe, 26 Dec 1984, 1 (AM W28965).

Description. Body fragile, slender; only anterior fragments examined; longest anterior fragment 2.4 mm long, 0.3 mm wide, with 21 chaetigers; usually colourless, but some specimens with few dark transverse bands on dorsum of anterior segments, varying in intensity. Posterior to proventricle, segments fused, forming suprasegmental structures of 2–3 segments (Fig. 78A). Prostomium oval, with 4 eyes in open trapezoidal arrangement; antennae irregularly articulated, originating on anterior margin of prostomium, median antenna inserted slightly posteriorly behind lateral antennae (Figs 42D,E, 78A). Median antenna with about 15 articles, about twice combined length of prostomium and palps; lateral antennae about half length of median antenna, with about 6–8 articles. Palps blunt, similar in length to prostomium, free from each other, ventrally folded in several specimens (Figs 42E, 78B). Peristomium shorter than subsequent segments, forming small, indistinct occipital flap (Fig. 42C–E); dorsal tentacular cirri irregularly articulated, similar in length to median antenna; ventral tentacular cirri about half length of dorsal ones, almost smooth (Fig. 78A,B). Nuchal organs as 2 dorsal densely ciliated grooves between prostomium and peristomium (Figs 42D,E, 78A). Dorsal cirri of chaetiger 1 elongated, articulated, with about 13 irregular

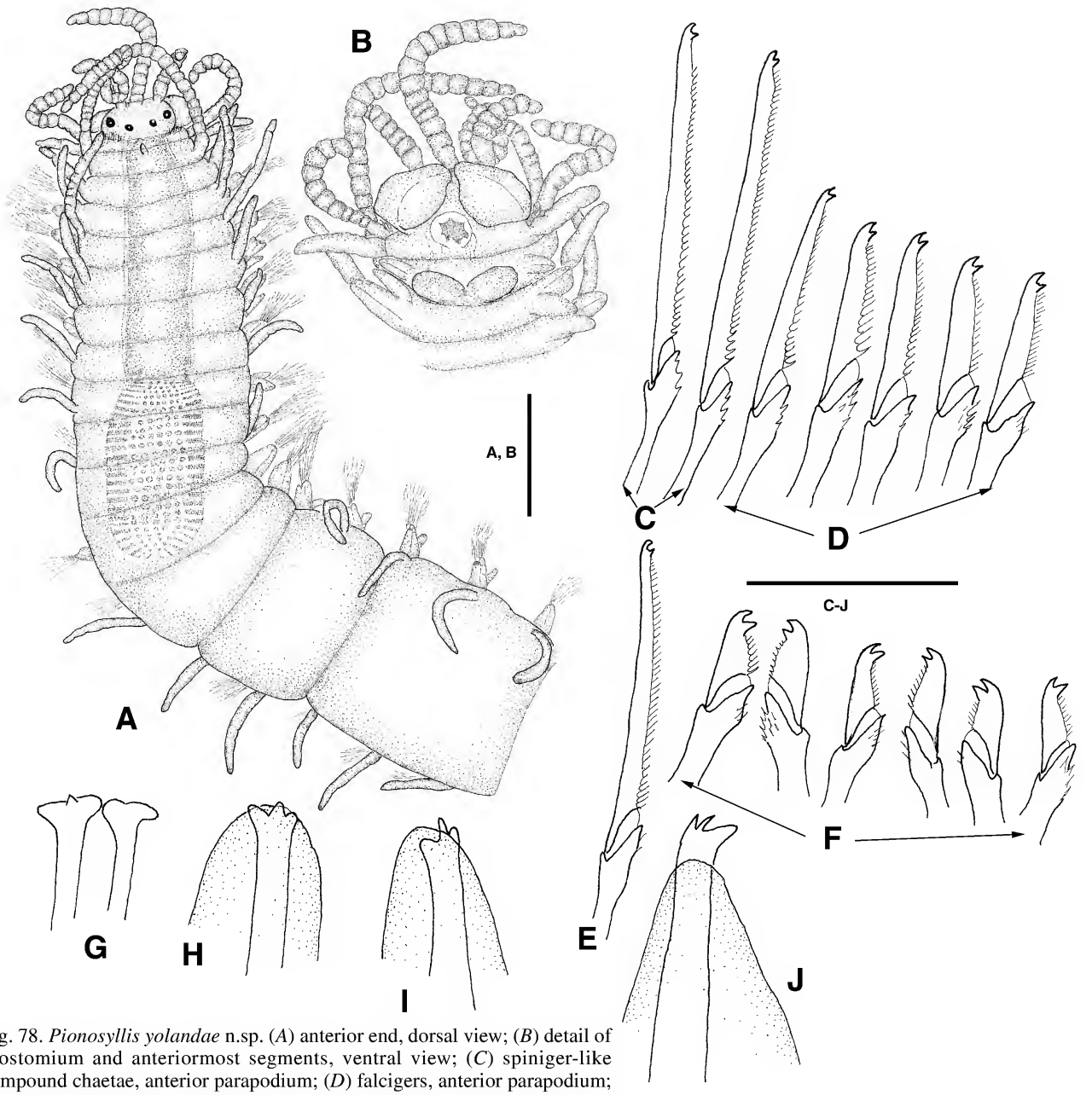


Fig. 78. *Pionosyllis yolandae* n.sp. (*A*) anterior end, dorsal view; (*B*) detail of prostomium and anteriormost segments, ventral view; (*C*) spiniger-like compound chaetae, anterior parapodium; (*D*) falcigers, anterior parapodium; (*E*) spiniger-like compound chaeta, midbody; (*F*) falcigers, midbody; (*G–J*) gradation on number and shape of aciculae from anterior parapodia to midbody. AM W28876. Scales: *A* 0.18 mm, *B* 97.5 μm, *C–J* 20 μm.

articulations; dorsal cirri of remaining anterior parapodia slightly elongated, rugose, shorter than body width, becoming progressively shorter and smooth along body; midbody dorsal cirri alternating in length, longer ones about half of length of body width, shorter ones about two thirds length of longer ones (Fig. 78A). Parapodial lobes conical; ventral cirri digitiform, slightly shorter than parapodial lobes; ventral cirri of chaetiger 1 leaf-like, enlarged, located mid ventrally (Fig. 78B). Anterior parapodia with about 2–3 compound chaetae with slender, spiniger-like blades bidentate, with short spines on margin (Figs 78C, 49A), blades about 36 μm in length; 8–10 compound falcigerous chaetae with distinctly shorter blades, similar in shape but slightly larger (Figs 78D, 49B), with dorsoventral gradation within fascicle, 22 μm in length dorsally, 15 μm in length ventrally. Progressively along body, number of compound chaetae with elongated blades decreases to 1–2 in midbody, 32 μm in length, remaining compound chaetae, about 6, with shorter and wider blades, about 10 μm in length, with prominent proximal tooth, similar in size to distal tooth or longer (Fig. 78E,F). Dorsal and ventral simple chaetae not seen. Anterior parapodia with 2 tricuspid aciculae (Fig. 78G), proventricular segments with single acicula, becoming progressively larger (Fig. 78H,I), extending beyond parapodial lobes, with large tooth and 2 smaller ones (Fig. 78J), similar in shape to subacicular hooks in eunicids (Fig. 49C). Pharynx proportionally long and slender (Fig. 78A), through 8–9 segments, anterior rim with crown of 10 soft papillae and layer of cilia (Fig. 42F); pharyngeal tooth small, located slightly behind anterior rim. Proventricle about half of pharynx length, with about 20 muscle cell rows. Details of posterior segments unknown.

Remarks. *Pionosyllis yolandae* n.sp. is similar to *Pionosyllis aciculata* San Martín, 1990, from Cuba; but, this latter species has much shorter compound chaetae, with typical dorsoventral gradation in length of blades within a fascicle, and lacks elongated, spiniger-like compound chaetae (San Martín, 1990). *Pionosyllis lamelligera* (Saint-Joseph, 1887) has spiniger-like chaetae, but it lacks the characteristic enlarged, tridentate aciculae, and the posterior falcigers have the proximal tooth longer than distal tooth present, whereas in *Pionosyllis yolandae* the teeth are of similar size (San Martín, 2003, for a description of *Pionosyllis lamelligera*).

Habitat. Occurring on gorgonaceans, ascidians, sponges, and in sand, from 14 to 244 m depths.

Distribution. Australia (New South Wales, Western Australia).

Etymology. The species is named after Miss Yolanda Lucas, who helped us in many ways, especially collaborating with us on the illustrations of this paper.

Pionosyllis sp.

Fig. 79A–G

?*Pionosyllis divaricata* Haswell, 1920: 104, pl. 13, figs 2, 3. Not Keferstein, 1862: 11.
?*Eusyllis* sp. Hartmann-Schröder, 1984: 19, fig. 27.

Material examined. AUSTRALIA: NEW SOUTH WALES: NE corner of Clark Is., Port Jackson, 33°51.85'S 151°14.7'E, within encrustation on outside of bottle, 4.5 m, coll. P.A. Hutchings, 17 Apr 1996, 1 anterior & 1 posterior fragment (AM W28410).

Description. Both fragments in poor condition; anterior fragment of 19 segments and mid-posterior fragment of 8 segments. Similar to *Pionosyllis rousei*, but compound chaetae more elongate, with longer spiniger-like chaetae and elongated falcigers; anterior parapodia with numerous compound chaetae, blades of spiniger-like chaetae about 69 µm long, bidentate, both teeth small and equal in size (Fig. 79A); falcigers with blades 45–49 µm in length, proximal tooth distinctly curved but lacking tendon (Fig. 79B). Midbody parapodia with some spiniger-like chaetae, blades about 89 µm in length, teeth distinctly hooked, but lacking tendon (Fig. 79C); falcigers with blades 40–51 µm in length, most provided with tendon (Fig. 79D). Posterior parapodia with single spiniger-like chaetae, long and slender, blades 90 µm in length, with proximal tooth distinctly curved, indistinct tendon (Fig. 79E); falcigers with both teeth marked, curved, proximal tooth longer than distal tooth, with distinct tendon between proximal tooth and blade edge (Fig. 79F) 42–58 µm in length. Dorsal and ventral simple chaetae not seen. Aciculae distally blunt, with short pointed tip; 2 acicula on anterior parapodia (Fig. 79G), and 1 on posterior parapodia (Fig. 79H). Pharynx everted, with crown of 10 long, slender soft papillae, pharyngeal tooth located near anterior margin of pharynx. Proventricle short and wide, through 10 segments, with about 27 muscle cell rows.

Remarks. This species does not agree with any other described species within the genus *Pionosyllis*. Additional complete material, however, is necessary before it can be described as new species.

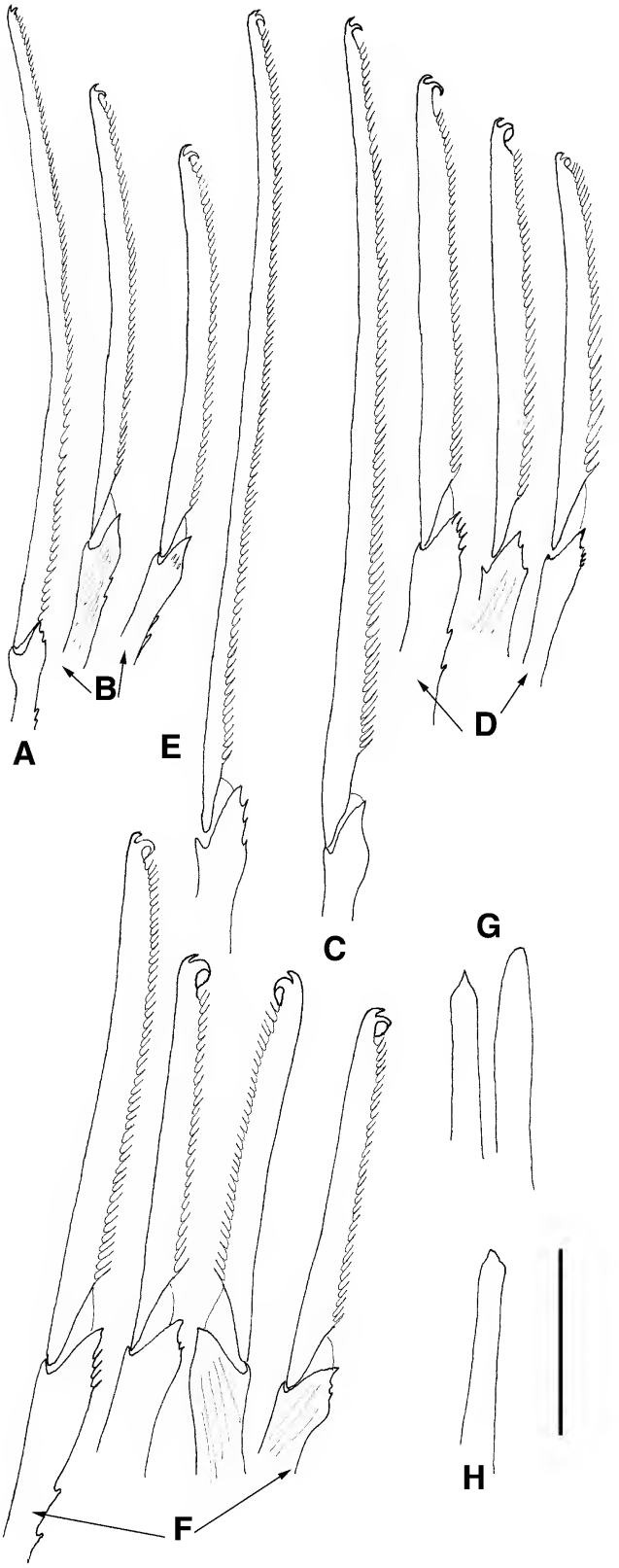
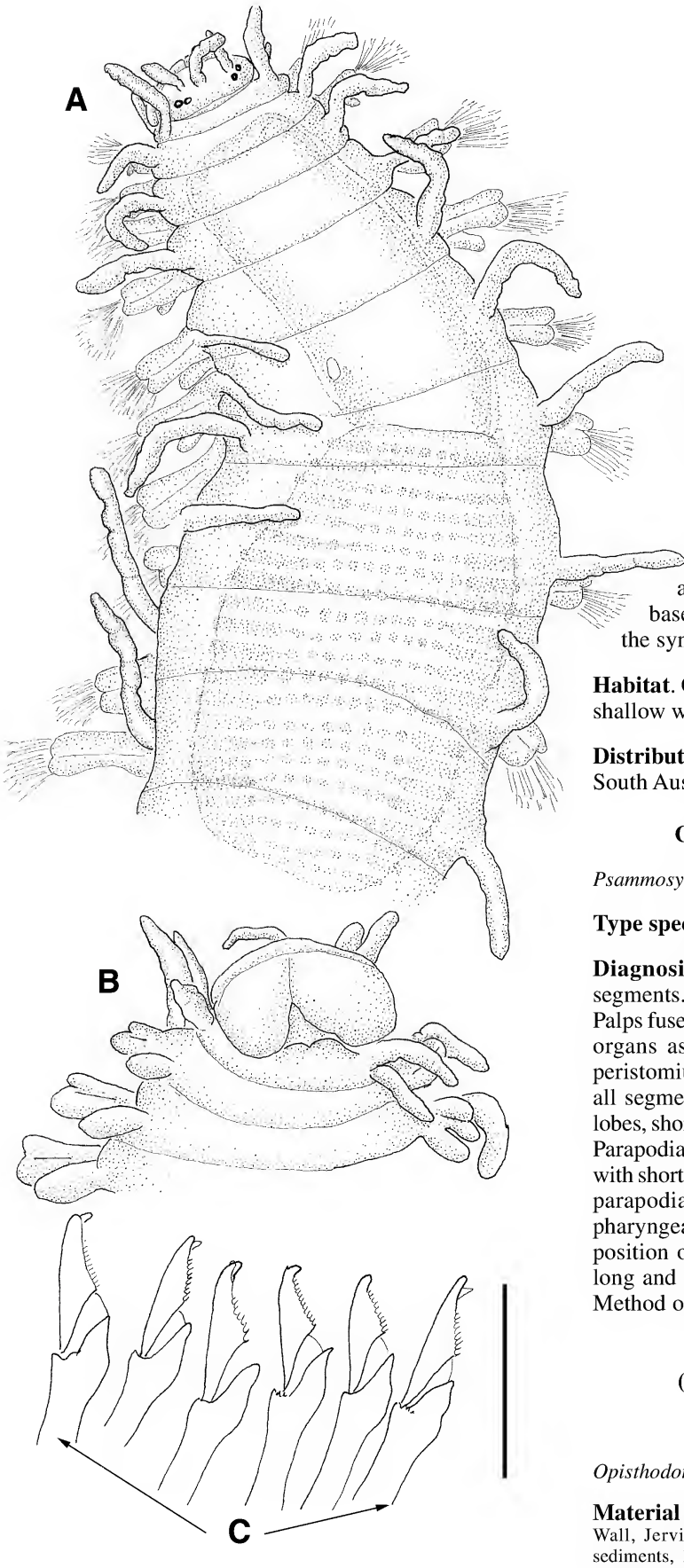


Fig. 79. *Pionosyllis* sp. (*A*) spiniger-like compound chaeta, anterior parapodium; (*B*) falcigers, anterior parapodium; (*C*) spiniger-like compound chaeta, midbody; (*D*) falcigers, midbody; (*E*) spiniger-like compound chaeta, posterior parapodium; (*F*) falcigers, posterior parapodium; (*G*) aciculae, anterior parapodium; (*H*) acicula, posterior parapodium. AM W28410. Scale: 20 µm.



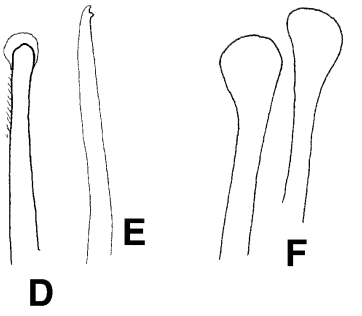


Fig. 80. *Psammosyllis curticirris* (Hartmann-Schröder, 1983) n.comb. (*A*) anterior end, dorsal view; (*B*) anterior end, ventral view; (*C*) compound chaetae, midbody; (*D*) dorsal simple chaeta; (*E*) ventral simple chaeta; (*F*) aciculae, midbody. AM W24704. Scales: *A* 0.1 mm, *B* 0.18 mm, *C–F* 20 µm.

Material described by Haswell as *Pionosyllis divaricata* could not be located for examination, and therefore possible identity of this species is based only on the description and this is reflected in the synonymies.

Habitat. Cryptic species on encrusting organisms found in shallow water.

Distribution. Australia (New South Wales and possibly South Australia).

Genus *Psammosyllis* Westheide, 1990

Psammosyllis Westheide, 1990: 165.

Type species. *Psammosyllis aliceae* Westheide, 1990.

Diagnosis. Body small, of meiofaunal size, with few segments. Prostomium with 4 eyes, and 3 short antennae. Palps fused entire length or just leaving distal notch. Nuchal organs as 2 ciliated grooves between prostomium and peristomium. Two pairs of tentacular cirri. Dorsal cirri on all segments, smooth, cylindrical, longer than parapodial lobes, shorter than body width. Ventral cirri digitiform, short. Parapodial lobes bilobed. Compound chaetae heterogomph, with short blades. Dorsal and ventral simple chaetae on some parapodia. Pharynx wide, without papillae on opening, pharyngeal tooth stout, small, located posteriorly on lateral position of pharynx. Proventricle massive, barrel-shaped, long and large. Pygidium with 2 long, filiform anal cirri. Method of reproduction unknown.

Psammosyllis curticirris (Hartmann-Schröder, 1983) n.comb.

Fig. 80A–F

Opisthodonta curticirris Hartmann-Schröder, 1983: 130, figs 11–14.

Material examined. AUSTRALIA: NEW SOUTH WALES: Hole-in-the-Wall, Jervis Bay, 35°07.6'S 150°44.8'E, sandy mud, unvegetated sediments, 12 m, coll. P.A. Hutchings & party, 18 Aug 1989, 1 (AM W24706). Paratype WESTERN AUSTRALIA: Dunsborough, 33°36'S 115°06'E, fine sand, intertidal, coll. G. Hartmann-Schröder, 9 Nov 1975, (AM W196215).

Description. Body proportionally broad in relation to other species of genus, 3.1 mm long, 0.4 mm wide, with 29 segments. Prostomium oval, width more than twice length; 2 pairs of eyes in open trapezoidal pattern, close to each other, laterally inserted; antennae shorter than combined length of prostomium and palps (Fig. 80A), slightly rugose, median antenna originating between anterior eyes, slightly longer than lateral antennae; lateral antennae shorter than prostomium, inserted near anterior margin of prostomium. Palps broad, fused for almost entire length, except for distinct terminal notch, ventrally folded on one specimen (Fig. 80B). Peristomium shorter than following segments; dorsal tentacular cirri longer than median antenna, similar in shape, ventral tentacular cirri shorter than dorsal ones. Dorsal cirri smooth, similar to antennae and tentacular cirri, rough, slightly enlarged on middle, tapered basally and distally, longer than parapodial lobes (Fig. 80A), shorter than half of body width. Parapodial lobes broad, bilobed dorsally (Fig. 80A). Ventral cirri short, oblong, shorter than parapodial lobes. Compound chaetae similar throughout, heterogomph falcigers, blades short, about 12–14 μm in length, short spines on margin, some apparently unidentate, others with prominent proximal tooth located on different plane (Fig. 80C), about 20–25 per parapodium. Dorsal simple chaetae from anterior segments, unidentate, distally knobbed and provided with small transparent hood and short spines on margin (Fig. 80D). Ventral simple chaetae on posterior chaetigers, smooth, bidentate, both teeth similar (Fig. 80E). Aciculae distally knobbed (Fig. 80F), 3 present anteriorly, decreasing to 1 on most posterior chaetigers. Pharynx wide, through 5–6 segments, pharyngeal tooth located laterally, near proventricle (Fig. 80A). Proventricle barrel-shaped, massive, through 4–5 segments, with about 50 muscle cell rows.

Remarks. This species differs in several characters from the recently emended description of *Opisthodonta*, in having fused palps, short cirri, a massive proventricle and large pharynx without soft papillae as well as a pharyngeal tooth located laterally, not mid-dorsally; furthermore, *Opisthodonta* as redefined above is characterized by having ventral cirri of anteriormost segments expanded leaf-like, partially fused with parapodial lobes, whereas in this species the ventral cirri are short and ovoid. We are therefore transferring *Opisthodonta curticirris* Hartmann-Schröder to the genus *Psammosyllis* as the above characters clearly place it in this genus rather than the emended genus *Opisthodonta*. The genus *Psammosyllis* contains only two other previously described species *P. aliceae* Westheide, 1990, described from India, and *P. wui* Ding & Westheide, 1997, described from China. *Psammosyllis curticirris* differs from these two species by having a broader body, dorsal simple chaetae with a distal hood, and compound chaetae with blades unidentate or bidentate with both teeth on different planes (see Westheide, 1990; Ding & Westheide, 1997). This represents the first record of the genus in Australia.

Habitat. Occurring in sandy substrates, from intertidal to shallow depths.

Distribution. Australia (Western Australia, New South Wales).

Genus *Streptodonta* n.gen.

Type species. *Opisthodonta pterochaeta* Southern, 1914, herein designated.

Diagnosis. Body long, slender, tapered anteriorly and posteriorly, with numerous segments. Prostomium pentagonal to triangular, with 4 eyes and 2 anterior eyespots. Three antennae. Palps short, fused basally, triangular in shape. Nuchal organs as 2 ciliated grooves between peristomium and prostomium. Two pairs of tentacular cirri. Antennae, tentacular and dorsal cirri elongated, smooth, distally tapered. Ventral cirri triangular. Compound chaetae with translucent hood on margin, ornamented with several rows of minute spines. Dorsal simple chaetae with translucent hood. Ventral simple chaetae probably absent. Aciculae of several anterior parapodia distinctly enlarged. Pharynx and proventricle long, pharyngeal tooth located laterally and distinctly posteriorly, close to proventricle. Reproduction by epigamy.

Remarks. The species *Opisthodonta pterochaeta* differs in several characters from the emended diagnosis of *Opisthodonta*, such as having palps fused basally, pharyngeal tooth located laterally, extremely long pharynx and proventricle, and, also having enlarged aciculae on several anterior segments and with different types of chaetae. As suggested by Kudenov & Harris (1995), a new genus was needed for this species.

Streptodonta n.gen., is similar to *Streptosyllis* in having enlarged aciculae on some anterior parapodia, but differs in having a pharyngeal tooth, much longer pharynx and proventricle, and in the shape of the compound chaetae.

It is probably more closely related to *Psammosyllis* Westheide, 1990, than to *Opisthodonta*, sharing with the former some unusual characters, such as the position of the pharyngeal tooth (see Westheide, 1990).

Etymology. The name of the new genus is a combination of the prefix *streptos*, from the Greek, meaning twisted, (in reference to *Streptosyllis*), and the suffix *donta*, (in reference to *Opisthodonta*), because it shares characters of both genera, thick, enlarged aciculae, like those present in *Streptosyllis* and a posterior pharyngeal tooth, like those present in *Opisthodonta*.

Streptodonta pterochaeta (Southern, 1914), n.comb.

Fig. 81E

Opisthodonta pterochaeta Southern, 1914: 30, pl. IV, figs 6A–G.—Fauvel, 1923: 274, fig. 102d–i.—Hartmann-Schröder, 1971: 104, figs 4–6; 1996: 160.—Campoy, 1982: 304, pl. 24.—Bachelet, 1990: 174, fig. 1.—Parapar *et al.*, 1993: 370, fig. 4.—San Martín, 2003: 51, figs 13, 14.

Material examined. AUSTRALIA: NEW SOUTH WALES: Bass Point, 34°36'S 150°54'E, 50 m, 1 Feb 1990, 1 (AM W22989).

Description. Body slender, with numerous segments. Incomplete specimen, 4.2 mm long, 0.4 mm wide, with 31 chaetigers; an entire individual, may reach 10 mm or more. Prostomium pentagonal to triangular, with 2 pairs of eyes arranged in open trapezoidal pattern, and 2 anterior eyespots (Fig. 81A). Median antenna inserted between anterior eyes, slightly longer than combined length of prostomium and

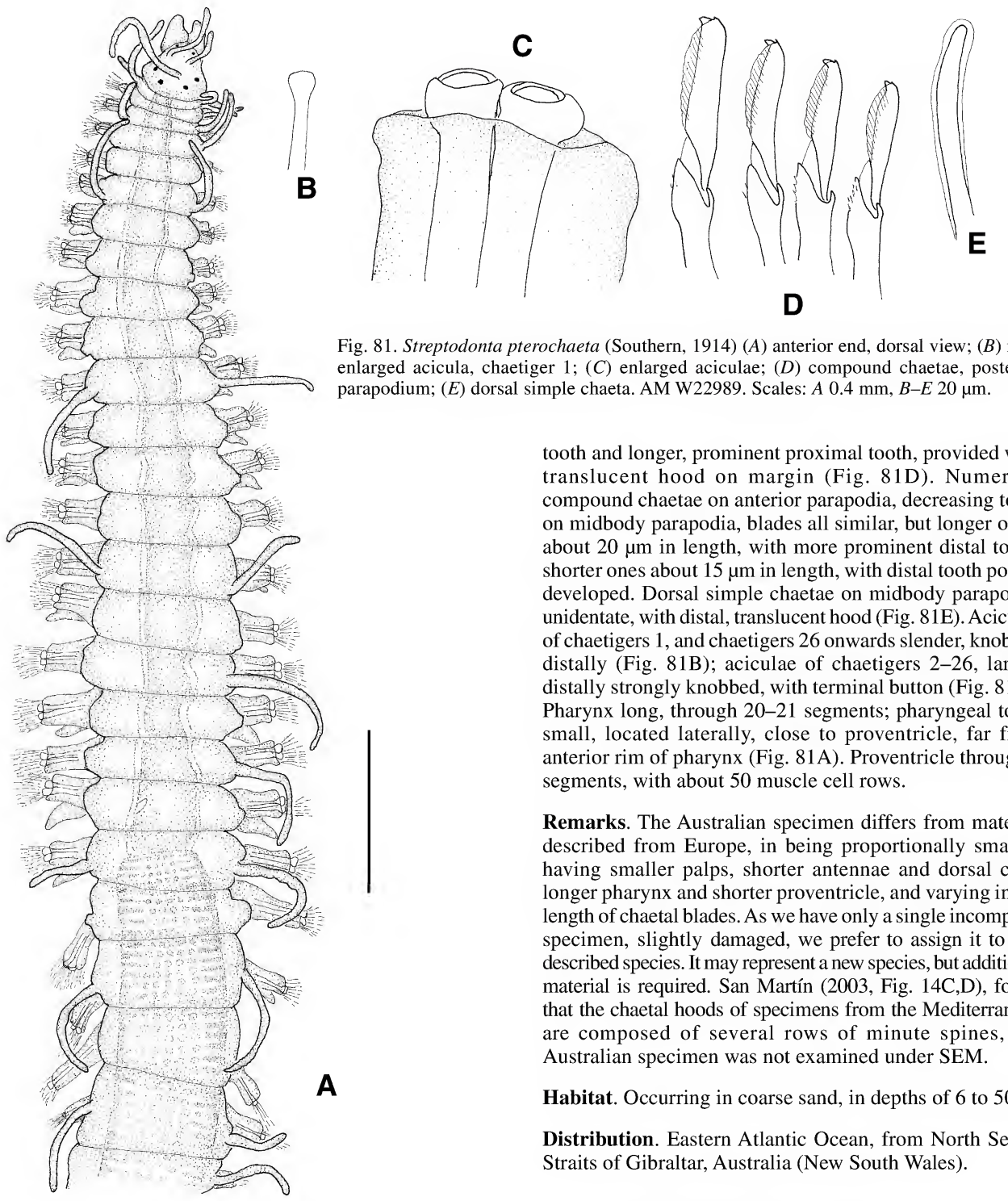


Fig. 81. *Streptodonta pterochaeta* (Southern, 1914) (*A*) anterior end, dorsal view; (*B*) non-enlarged acicula, chaetiger 1; (*C*) enlarged aciculae; (*D*) compound chaetae, posterior parapodium; (*E*) dorsal simple chaeta. AM W22989. Scales: *A* 0.4 mm, *B–E* 20 μm.

palps, lateral antenna in front of anterior eyes. Palps small, triangular, basally fused, shorter than prostomium (Fig. 81A). Peristomium slightly shorter than following segments; dorsal tentacular cirri longer than lateral antennae, shorter than median, ventral tentacular cirri shorter than dorsal ones. Dorsal cirri similar in shape to antennae and tentacular cirri, smooth, elongated, relatively short, shorter than body width (Fig. 81A), detached on most parapodia. Ventral cirri triangular, similar in length to parapodial lobes. Compound chaetae heterogomph falcigers, blades with indistinct distal tooth and longer, prominent proximal tooth, provided with translucent hood on margin (Fig. 81D). Numerous compound chaetae on anterior parapodia, decreasing to 10 on midbody parapodia, blades all similar, but longer ones, about 20 μm in length, with more prominent distal tooth, shorter ones about 15 μm in length, with distal tooth poorly developed. Dorsal simple chaetae on midbody parapodia, unidentate, with distal, translucent hood (Fig. 81E). Aciculae of chaetigers 1, and chaetigers 26 onwards slender, knobbed distally (Fig. 81B); aciculae of chaetigers 2–26, larger, distally strongly knobbed, with terminal button (Fig. 81C). Pharynx long, through 20–21 segments; pharyngeal tooth small, located laterally, close to proventricle, far from anterior rim of pharynx (Fig. 81A). Proventricle through 7 segments, with about 50 muscle cell rows.

Remarks. The Australian specimen differs from material described from Europe, in being proportionally smaller, having smaller palps, shorter antennae and dorsal cirri, longer pharynx and shorter proventricle, and varying in the length of chaetal blades. As we have only a single incomplete specimen, slightly damaged, we prefer to assign it to this described species. It may represent a new species, but additional material is required. San Martín (2003, Fig. 14C,D), found that the chaetal hoods of specimens from the Mediterranean are composed of several rows of minute spines, the Australian specimen was not examined under SEM.

Habitat. Occurring in coarse sand, in depths of 6 to 50 m.

Distribution. Eastern Atlantic Ocean, from North Sea to Straits of Gibraltar, Australia (New South Wales).

Genus *Streptosyllis* Webster & Benedict, 1884

Streptosyllis Webster & Benedict, 1884: 711.

Type species. *Streptosyllis arenae* Webster & Benedict, 1884, by monotypy.

Diagnosis. Body small (<5 mm in length), with up to about 40 chaetigers, usually 20–30. Prostomium with 4 eyes and 2 anterior eyespots. Three antennae. Palps fused at bases, without median furrow, sometimes terminating with 2 papillae, occasionally reduced and only papillae visible. Nuchal organs as 2 ciliated grooves between prostomium

and peristomium. Dorsal cirri usually smooth or indistinctly articulated, club-shaped to elongated, sometimes with glandular inclusions. Ventral cirri digitiform, sometimes distinctly longer than parapodial lobes and pseudo-articulated, arising from middle of parapodial lobes. Compound chaetae, homogomph to hemigomph, blades falcigerous or, exceptionally, some spiniger-like chaetae. Dorsal simple chaetae present usually from chaetiger 1. Ventral simple chaetae absent. Aciculae from some anterior parapodia distinctly enlarged. Pharynx unarmed, provided with crown of soft papillae. Proventricle with poorly defined muscle cell rows. Reproduction by epigamy (Garwood, 1991).

Key to Australian species of *Streptosyllis*

1 Palps reduced to 2 small papillae (Fig. 82A). Compound chaetae similar throughout ..... *S. aequiseta*

—— Palps not reduced to papillae. Compound chaetae of some anterior parapodia with distinctly different chaetae to those of remaining parapodia, with short blades 2

2 Enlarged aciculae and chaetae with short blades on chaetigers 2–4 (Fig. 84B). Blades of compound chaetae all unidentate (Fig. 84E). Palps with distal articulation ..... *S. biarticulata*

—— Enlarged aciculae on chaetigers 2–6 and chaetae with short blades on chaetigers 2–6. Compound chaetae with both unidentate and bidentate blades. Palps without distal articulation ..... *S. magnapalpa*

Streptosyllis aequiseta Hartmann-Schröder, 1981

Figs 82A–I, 83A–F

Streptosyllis aequiseta Hartmann-Schröder, 1981: 32, figs 53–58; 1983: 131, fig. 15; 1984: 21; 1985: 70; 1989: 26.— Böggemann *et al.*, 2003: 21, figs 3, 4.

Material examined. AUSTRALIA: NEW SOUTH WALES: Weeney Bay, Botany Bay, 34°01.3'S 151°09.7'E, mud, 1 m, coll. A. Roach & A. Jones, 30 Mar 1995, 1 (AM W23562); Weeney Bay, Botany Bay, 34°01.3'S 151°09.7'E, mud, 1 m, coll. A. Roach & A. Jones, 30 Mar 1995, 1 (AM W23567). WESTERN AUSTRALIA: Bush Bay, 30 km S of Carnarvon, 25°10'S 113°39'E, lumps of algae on shallow sandflats, intertidal, coll. H.E. Stoddart, 6 Jan 1984, 2 (AM W27654); inshore limestone reef, Ned's Camp, Cape Range National Park, 21°59'S 113°55'E, fine sediment & sand from patches in reef, 1 m, coll. H.E. Stoddart, 2 Jan 1984, 2 (AM W26782); N end of beach, Bundegi Reef, Exmouth Gulf, 21°49'S 114°11'E, rocky rubble, coralline algae with green epiphyte, 1.5 m, coll. H.E. Stoddart, 4 Jan 1984, 1 on SEM stub (AM W28370).

Description. Up to 4.9 mm long for 36 chaetigers (mature specimen), but usually smaller; examined specimens up to 1.4 mm long, 0.2 mm wide, with 23 chaetigers; fragile, often broken and damaged. Prostomium oval, with 4 eyes arranged in an open trapezoidal pattern and 2 anterior eyespots (Fig. 82A). Antennae smooth, club-shaped, similar in length to prostomium or longer, median antenna inserted between anterior eyes, lateral antennae inserted near eyespots. Palps reduced to 2 small, sometimes indistinct papillae (Figs 82A, 83B). Peristomium shorter than subsequent segments; tentacular cirri similar to antennae, dorsal ones slightly longer than ventral tentacular cirri. Dorsal cirri similar in shape and size to antennae (Fig. 82A) with distinct cirrophores. Parapodial lobes elongated, subrectangular, ending as rounded lobe (Fig. 82B), those of chaetigers 2–6 enlarged and truncated distally. Ventral cirri digitiform, elongated, longer than parapodial lobes, arising from about middle of ventral side of parapodial lobes (Figs 82B, 83A). Compound chaetae with homogomph articulations on anterior parapodia (Figs 82C,D, 83D), and hemigomph on mid to posterior parapodia (Figs 82F, 83C), provided with distinct subdistal spine on shafts, and bidentate blades, with short spines on margin. Anterior parapodia with 2 compound chaetae with elongate blades, about 21 µm long, distinctly bidentate, both teeth well separated (Figs 82C, 83D), and 6 compound chaetae with shorter blades (Fig. 82D), within fascicle blades 10 µm in length dorsally, 6 µm in length ventrally; difference between 2 types of chaetae becoming progressively less marked along body; posterior parapodia with 6 compound chaetae (Fig. 82F), bidentate with short spines on margin, dorsoventral gradation in length of blades within fascicle, 25 µm long dorsally, 9 µm long ventrally. Dorsal simple chaetae from chaetiger 1, unidentate, with minute serration on margin and distinct concave, translucent hood, covering tip of chaetae, small on simple chaetae of anterior parapodia (Figs 82E, 83E) but becoming more developed posteriorly (Figs 82G,H, 83F). Aciculae knobbed at tips, enlarged on chaetigers 2–6 (Fig. 82I). Pharynx extending through 3–4 segments, with crown of 10 soft papillae on margin (Fig. 83A). Proventricle large, pyriform, extending through about 6 segments and 40–48 indistinct muscle cell rows. Pygidium small, with 2 anal cirri and median papilla.

Remarks. All Australian specimens have all dorsal cirri smooth; those from the Seychelles (Böggemann *et al.*, 2003) have longer dorsal cirri, articulated, with two glands on each article, except anteriormost, which are smooth. Until more material is available, it is unknown as to the levels of variation of articulation of dorsal cirri that may occur within a species. So at this stage we are tentatively accepting the records of this species from the Seychelles.

Habitat. Occurring interstitially in coralline sand, fine sand, mud, on algae, from intertidal to shallow depths.

Distribution. Australia (Western Australia, South Australia, Tasmania, New South Wales), possibly Seychelles Islands.

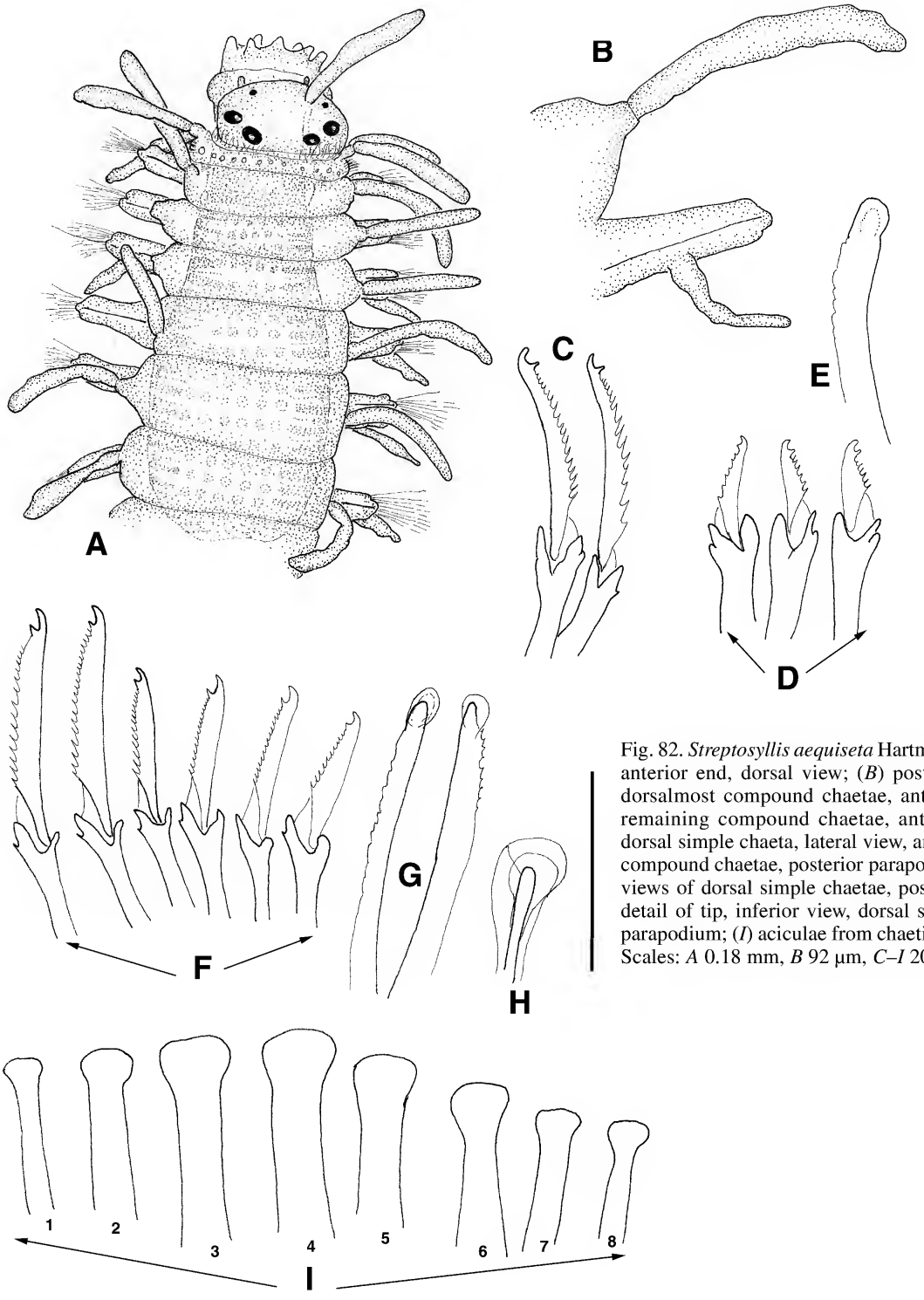


Fig. 82. *Streptosyllis aequiseta* Hartmann-Schröder, 1981 (*A*) anterior end, dorsal view; (*B*) posterior parapodium; (*C*) dorsalmost compound chaetae, anterior parapodium; (*D*) remaining compound chaetae, anterior parapodium; (*E*) dorsal simple chaeta, lateral view, anterior parapodium; (*F*) compound chaetae, posterior parapodium; (*G*) two different views of dorsal simple chaetae, posterior parapodium; (*H*) detail of tip, inferior view, dorsal simple chaeta, posterior parapodium; (*I*) aciculae from chaetigers 1–8. AM W28370. Scales: *A* 0.18 mm, *B* 92 μm, *C–I* 20 μm.

Streptosyllis biarticulata Hartmann-Schröder, 1991

Fig. 84A–F

Streptosyllis biarticulata Hartmann-Schröder, 1991: 36, figs 57–61.

Material examined. AUSTRALIA: QUEENSLAND: Heron Is., Great Barrier Reef, 23°27'S 151°55'E, coarse sand, intertidal, 4 Feb 1976, coll. G. Hartmann-Schröder, holotype (HZM P-20545).

Description. Body 2.5 mm long, 0.2 mm wide, with 35 chaetigers, incomplete specimen. Prostomium oval, with 4 large eyes in trapezoidal arrangement. Antennae broken (and not in vial); point of insertion not visible. Palps shorter than prostomium, fused basally. Peristomium well defined, shorter than following segments; dorsal tentacular cirri with about 6 articles, ventral tentacular cirri smooth, shorter than dorsal ones. Most dorsal cirri detached; dorsal cirri with 4–7 articles. Enlarged aciculae (Fig. 84C) from chaetigers 2–

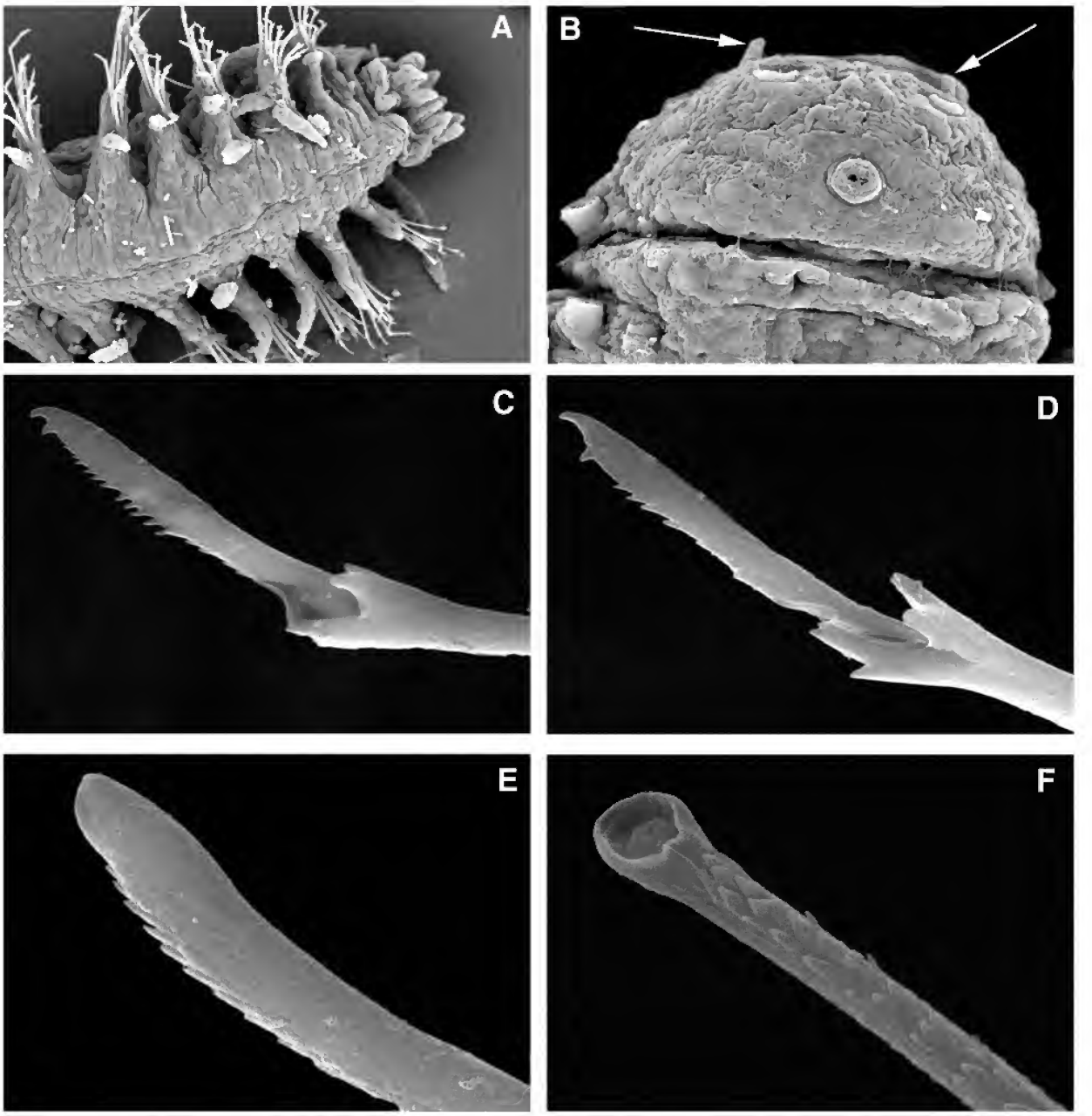


Fig. 83. SEM of *Streptosyllis aequiseta* Hartmann-Schröder, 1981. (*A*) anterior end, ventral view; (*B*) detail of prostomium, showing the papillae of palps; (*C*) dorsal compound chaeta, posterior parapodium; (*D*) same, anterior parapodium; (*E*) dorsal simple chaeta, anterior parapodium, lateral view; (*F*) dorsal simple chaeta, inferior view, posterior parapodium. AM W28370.

4, large basally, distally blunt. Subsequent aciculae and aciculae of chaetiger 1, similar but much thinner (Fig. 84F). Compound chaetae with thick shafts, some of them provided with thin hood distally, and blades distally blunt, unidentate, with short spines on margin, and slight dorsoventral gradation in length of blades within fascicle (Fig. 84E), 13 µm in length dorsally, 7 µm in length ventrally. Compound chaetae of chaetigers 3–4 with distinctly shorter blades, blunt, short, with thick shafts, some covered by translucent hood (Fig. 84B). Dorsal simple chaetae from chaetiger 1, thick, distally blunt, with hood, longitudinally striated (Fig. 84A), becoming thicker posteriorly (Fig. 84D). Ventral simple chaetae absent. Pharynx extends for about 4 segments. Proventricle extending for 3.5 segments, with about 35 muscle cell rows.

Habitat. Occurring in coral sand, intertidally.

Distribution. Australia (Queensland).

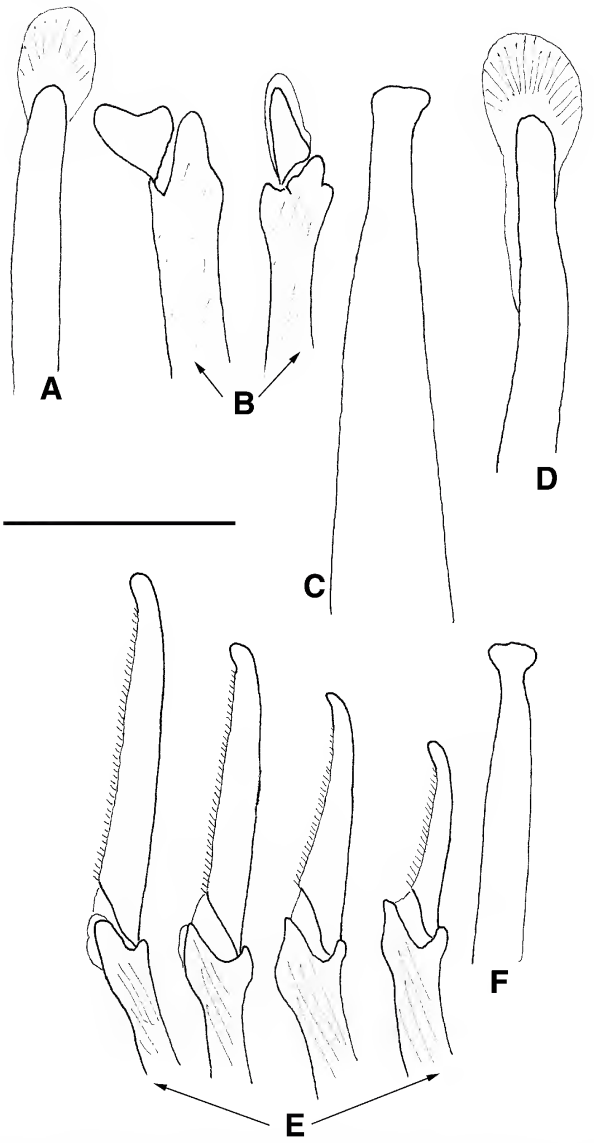


Fig. 84. *Streptosyllis biarticulata* Hartmann-Schröder, 1991 (*A*) dorsal simple chaeta, anterior parapodium; (*B*) compound chaetae from parapodia 2–4; (*C*) enlarged acicula (chaetigers 2–4); (*D*) dorsal simple chaeta, midbody; (*E*) compound chaetae, midbody; (*F*) acicula, midbody. ZMH P-20545. Scale: 20 μm.

Streptosyllis magnapalpa Hartmann-Schröder, 1981

Fig. 85A–H

Streptosyllis magnapalpa Hartmann-Schröder, 1981: 33, figs 59–67; 1982: 65, fig. 47; 1983: 13; 1987: 38.

Material examined. AUSTRALIA: WESTERN AUSTRALIA: Horrocks, algae, seagrass and sand, 28°23'S 114°26'E, intertidal, 17 Oct 1975, coll. G. Hartmann-Schröder, paratype (HZM P-16488); Cervantes, 30°30'S 115°03'E, fine sand and *Posidonia*, intertidal, coll. G. Hartmann-Schröder, 24 Oct 1975, 1 (HZM P-17019).

Description. Body fragile, without colour markings; largest complete specimen 2.8 mm long, 0.2 mm wide, with 37 chaetigers. Prostomium oval, with 4 eyes in open trapezoidal arrangement; tuft of cilia present in front of anterior eyes. Antennae short, smooth, slightly club-shaped; median antenna missing (broken and lost), arising on middle of prostomium; lateral antennae inserted near anterior margin of prostomium (Fig. 85A). Palps shorter than prostomium, fused basally. Peristomium slightly shorter than following segment, provided with some hyaline inclusions (Fig. 85A); tentacular cirri similar to lateral antennae in shape; dorsal tentacular cirri slightly longer than lateral antennae, ventral tentacular cirri shorter than dorsal. Transverse row of cilia on dorsum of each segment (Fig. 85A). Dorsal cirri of anterior 2–3 segments similar to antennae and tentacular cirri, although slightly longer. Subsequent dorsal cirri articulated, with few articles, 4–6, some of them with granular, dark inclusions. Aciculae slender, distally blunt (Fig. 85D); enlarged aciculae on chaetigers 2–6. Compound chaetae of chaetigers 2–6 with thick shafts, short, unidentate blades, some covered by translucent hood, with slight dorsoventral gradation in length of blades within fascicle, 18 μm in length dorsally, and 11 μm in length ventrally (Fig. 85C). Compound chaetae of subsequent chaetigers with elongate, unidentate, distally blunt blades, with short spines on margin, shafts with thick subdistal spine, and dorsoventral gradation in length within fascicle, 47 μm dorsally, 22 μm ventrally (Fig. 85F); progressively on following segments, blades becoming slender, and tips indistinctly bidentate (Fig. 85G). Anterior parapodia with about 6 compound chaetae, reducing to 4 on posterior parapodia. Dorsal simple chaetae from chaetiger 1, thick, distally blunt, with distal, longitudinally striated hood, similar throughout body (Fig. 85B,E,H). Pharynx long, through about 5–6 segments, with distal crown of 10 papillae and subdistal crown of much smaller papillae (Fig. 85A). Proventricle through about 5 segments, with 35 muscle cell rows. Pygidium small, with two long anal cirri and median short papilla.

Habitat. Occurring in algae, seagrass, sand, from intertidal to shallow depths.

Distribution. Australia (Western Australia, Victoria).

Genus *Syllides* Örsted, 1845

Syllides Örsted, 1845: 408.

Type species. *Syllides longocirrata* Örsted, 1845, designated by Hartman, 1959.

Diagnosis. Body small, short, with relatively few segments. Prostomium with 4 eyes, typically pair of anterior eyespots. Three antennae. Palps fused basally, without median furrow, sometimes ending with small papilla. Two pairs of tentacular cirri. Nuchal organs as 2 ciliated grooves between prostomium and peristomium. Antennae, tentacular cirri, and dorsal cirri of chaetigers 1 and 2, smooth, non-articulated, club-shaped to fusiform; dorsal cirri from chaetiger 3 onwards, distinctly articulated, with glandular inclusions on some articles. Ventral cirri digitiform. Compound chaetae heterogomph with blades slender, usually bidentate. Dorsal simple chaetae from anterior segments, usually from chaetiger 1. Ventral simple chaetae present in some species. Pharynx unarmed, with crown of soft papillae. Reproduction by epigamy, some species brood eggs ventrally (Heacox & Schroeder, 1978).

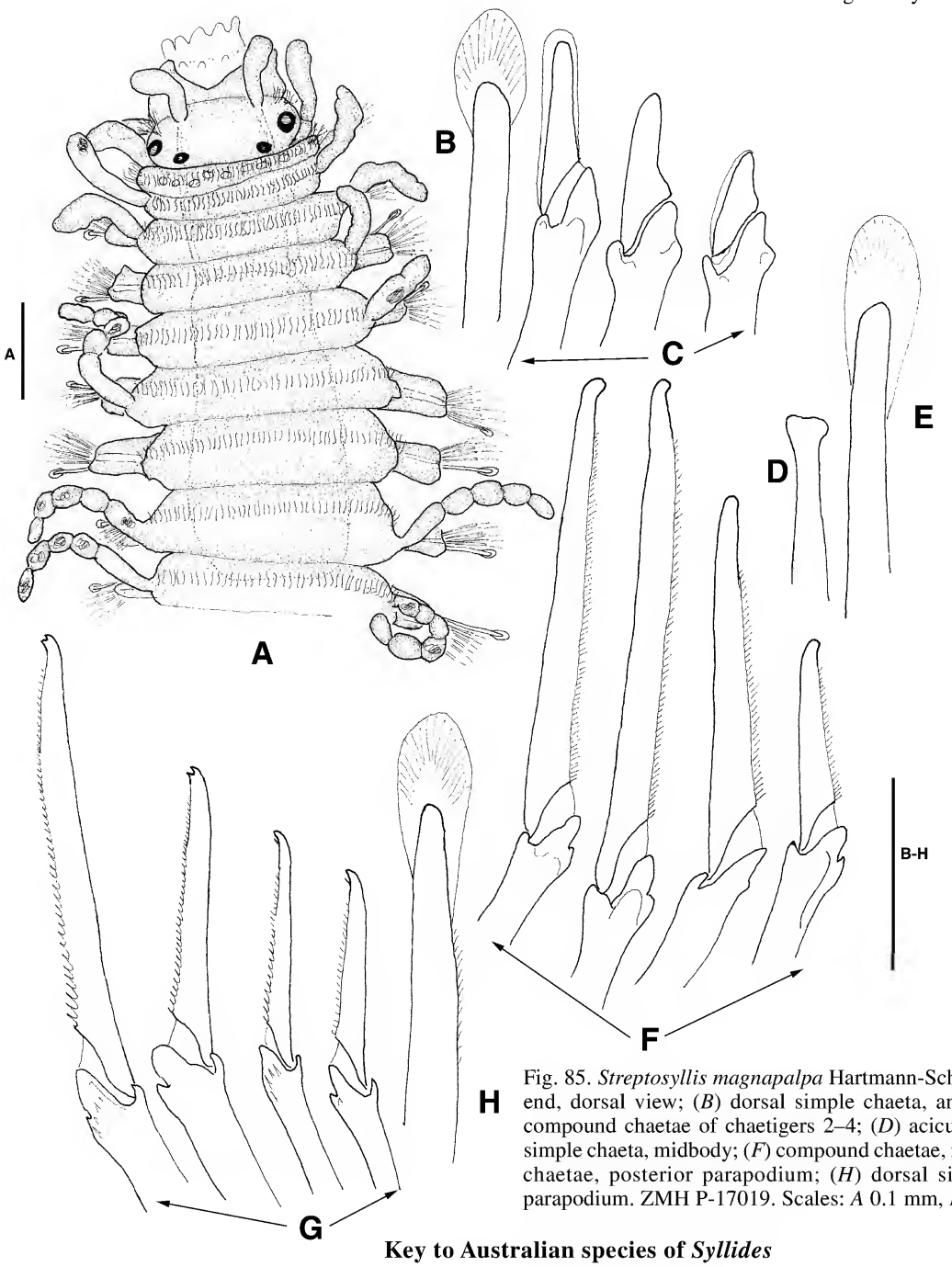


Fig. 85. *Streptosyllis magnapalpa* Hartmann-Schröder, 1981 (*A*) anterior end, dorsal view; (*B*) dorsal simple chaeta, anterior parapodium; (*C*) compound chaetae of chaetigers 2–4; (*D*) acicula, midbody; (*E*) dorsal simple chaeta, midbody; (*F*) compound chaetae, midbody; (*G*) compound chaetae, posterior parapodium; (*H*) dorsal simple chaeta, posterior parapodium. ZMH P-17019. Scales: *A* 0.1 mm, *B–H* 20 µm.

Key to Australian species of *Syllides*

1 Blades of some compound chaetae provided with long, basal spurs on margin (Fig. 89B) 2

—— Without basal spurs on blades of compound chaetae (Fig. 88D) 4

2 Longest blades of compound chaetae lacking basal spurs, only present on medium-length blades ..... *S. spinosus*

—— Longest blades of compound chaetae with basal spurs 3

3 Dorsal simple chaetae distally rounded, with distal hood (several rows of minute spines, under SEM) ..... *S. tam* n.sp.

—— Dorsal simple chaetae pointed, without hood ..... *S. japonicus*

4 Dorsal simple chaetae distally rounded, with distal hood (several rows of minute spines, under SEM). Proventricle long, through 4 segments ..... *S. pumilus*

—— Dorsal simple chaetae distally bifid, without hood. Proventricle short, through 2 segments ..... *Syllides* sp.

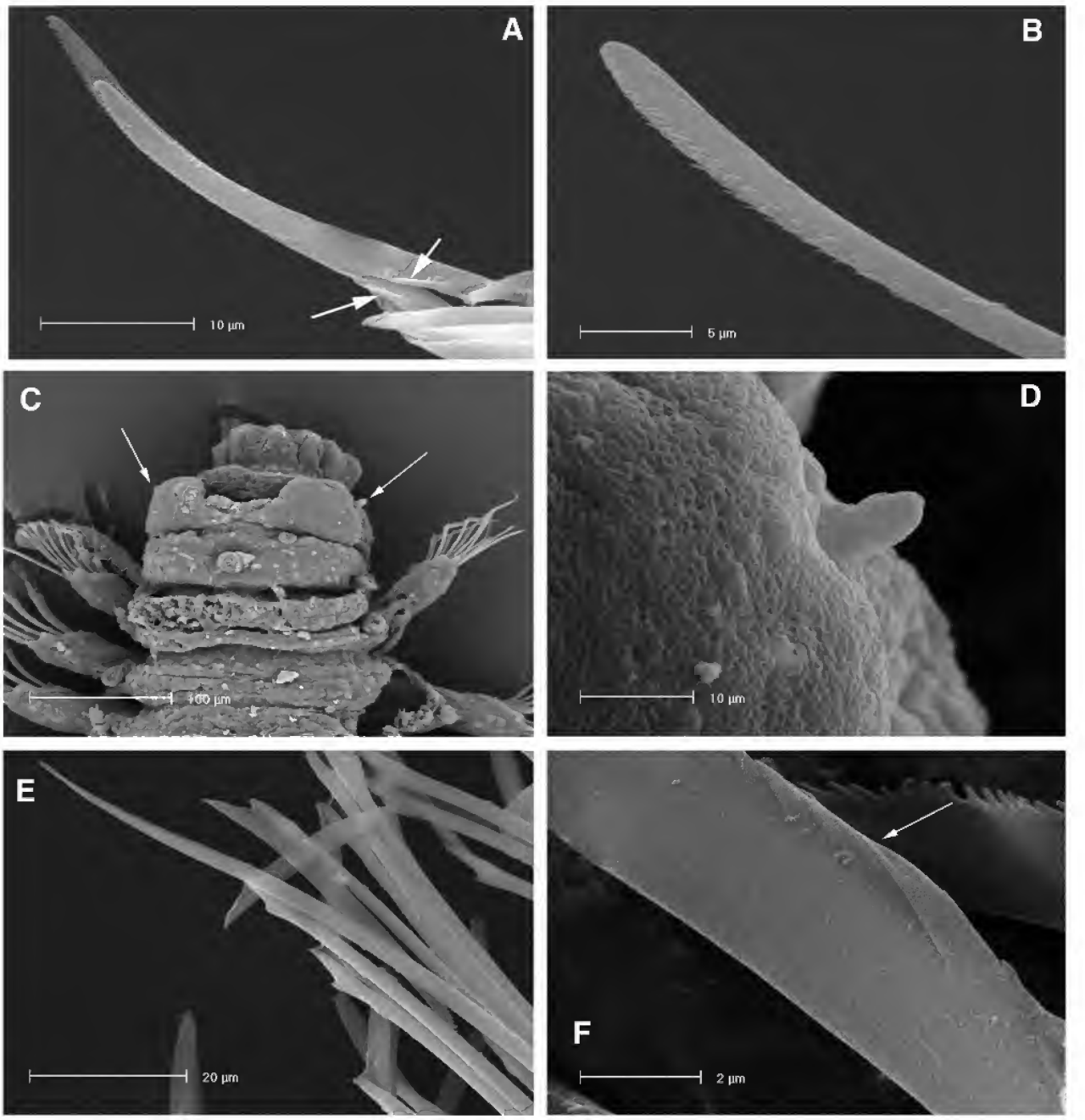


Fig. 86. SEM of *Syllides tam* n.sp. (*A*) compound chaetae of first and second pair (arrows showing basal spurs); (*B*) dorsal simple chaeta. SEM of *Syllides japonicus* Imajima, 1966 (*C*) anterior end, dorsal view (antennae and cirri missing; arrows showing papillae of palpi); (*D*) detail of papilla of palp; (*E*) dorsal simple chaeta and some compound chaetae; (*F*) detail of basal spur of compound chaeta. *A,B*: AM W196520; *C–F*: W23927.

Syllides japonicus Imajima, 1966

Figs 86C–F, 87A–E

Syllides japonicus Imajima, 1966: 112, text-fig. 36.—San Martín, 2003: 142, fig. 69.

Material examined. AUSTRALIA: NEW SOUTH WALES: 1 km SE of Dangar Is., Hawkesbury R., 33°33'S 151°14'E, shelly mud, 9 m, coll. A.R. Jones & party, 18 Dec 1979, 1 (AM W28467); Pittwater, 33°35.80'S 151°18.31'E, muddy sand, 14.4 m, coll. Australian Museum Party, 31 July 1995, 2 (AM W23927); 1 km SE of Dangar Is., Hawkesbury R., 33°33'S 151°14'E, shelly mud, 9 m, coll. A.R. Jones & party, 1 Aug 1979, 1 (AM W28975); 1.5 km SE of Dangar Is., Hawkesbury R., 33°33'S 151°14'E, sandy mud, 7 m, coll. A.R. Jones & party 18 Dec 1979, 1 (AM W28976). TASMANIA: Fancy Point, Bruny Is. 43°16'S 147°19'E, algae, 4 m, coll. G. Edgar, 10 Nov 1980, 1 (AM W18204). WESTERN AUSTRALIA: Inshore limestone reef, Ned's Camp, Cape Range National Park, 21°59'S 113°55'E, *Caulerpa* sp. algae, 1 m, coll. J.K. Lowry, 2 Jan 1984, 1 (AM W26739); Inshore limestone reef, Ned's Camp, Cape Range National Park, 21°59'S 113°55'E, small purple sponge with *Caulerpa* sp. algae & sticky sediment, 1.5 m, coll. R.T. Springthorpe, 2 Jan 1984, 2 (AM W26781).

Description. Body less than 5 mm in length, densely covered with golden inclusions on dorsum of each segment and prostomium (Fig. 87A). Prostomium oval, about twice as wide as long; 4 small eyes in open trapezoidal arrangement; antennae missing on most specimens, short, smooth. Palps broad, fused at bases, shorter than prostomium, each ending with distal, small papilla (Figs

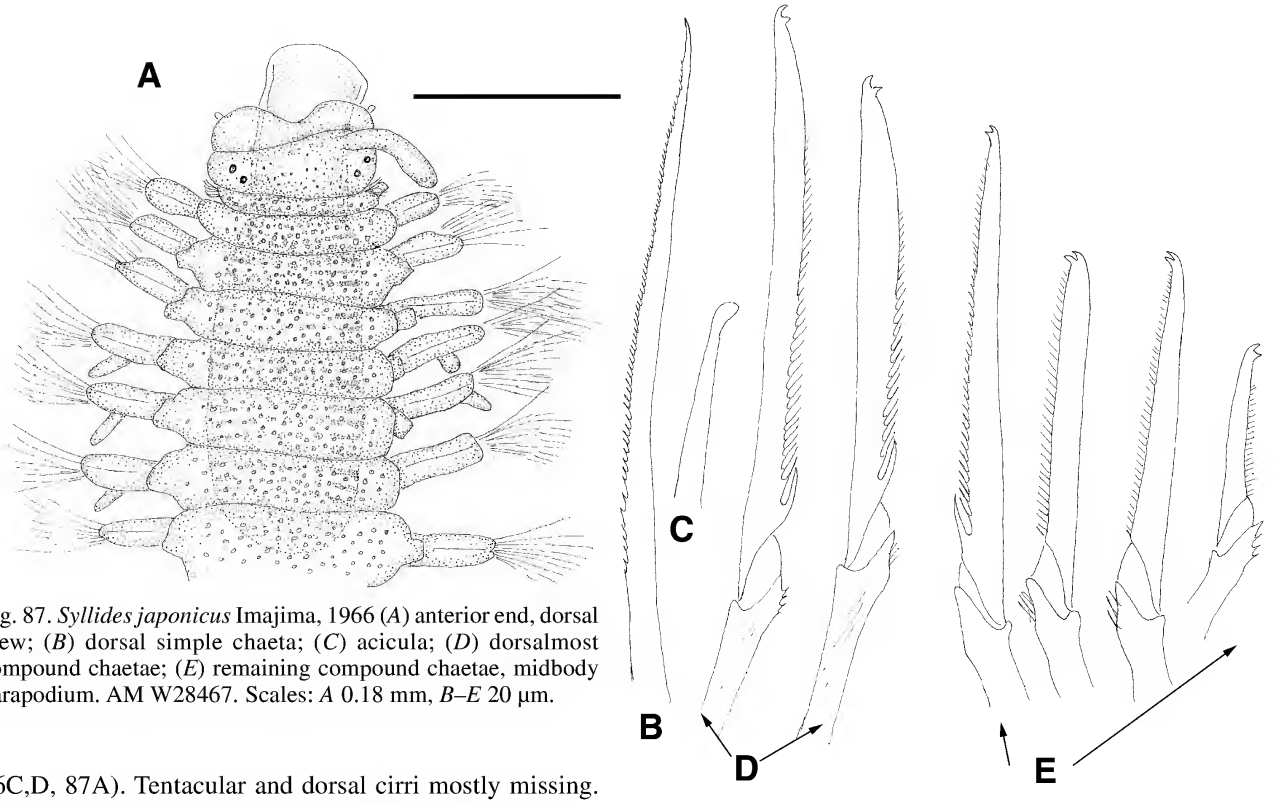


Fig. 87. *Syllides japonicus* Imajima, 1966 (*A*) anterior end, dorsal view; (*B*) dorsal simple chaeta; (*C*) acicula; (*D*) dorsalmost compound chaetae; (*E*) remaining compound chaetae, midbody parapodium. AM W28467. Scales: *A* 0.18 mm, *B–E* 20 µm.

86C,D, 87A). Tentacular and dorsal cirri mostly missing. Parapodia elongated, ventral cirri digitiform. Compound chaetae with elongated, distinctly bidentate blades, arranged in 5 pairs of chaetae within fascicle, each pair of similar shape and length; blades of dorsalmost pair with long blades, about 55 µm long, with basal long spur (Figs 86F, 87D) and short spines on margin; blades of subsequent pair similar (Fig. 87E) but shorter, about 44 µm long; remaining compound chaetae similar in shape, lacking basal spur (Fig. 87E), with dorsoventral gradation in length of blades, 35 µm in length dorsally and 22 µm in length ventrally. Dorsal simple chaetae from chaetiger 1, thin, pointed (Figs 86E, 87B), with short spines on margin (Fig. 87B). Ventral simple chaetae absent. Aciculae slender, distally knobbed (Fig. 87C) pharynx everted on most specimens, through about 4 segments when relaxed. Proventricle long, through 7 segments (Fig. 87A), with about 47 muscle cell rows.

Remarks. The original description of the species from Japan and descriptions of Mediterranean specimens do not describe the terminal papillae on the palps; these structures are small and could easily be overlooked. This species is characterized by having basal spurs on the bases of blades of the dorsalmost and second pair of compound chaetae; palps each with a small papilla on the Australian material, and dorsal simple chaetae, slender. *Syllides caribica* Licher, 1996, from Aruba Island in the Caribbean is similar, but differs in the following characters: the spurs on the compound chaetae are shorter, and have a smooth area between the spur and the edge of blade, the proventricle is shorter (through 2 segments), and the dorsal simple chaetae are slightly thicker (see Licher, 1996). *Syllides floridanus* Perkins, 1981 also has papillae on the palps, a long proventricle and slender, distally pointed dorsal simple chaetae; but the blades of the dorsalmost pair of compound chaetae lack basal spurs; they are present only on the second pair (Perkins, 1981).

All the material examined from Australia is damaged and while it closely resembles material examined from the Mediterranean, it may represent an undescribed species, but complete specimens are needed in order to confirm this.

Habitat. Occurring in sand, sandy mud, rhizomes of *Posidonia*, on algae and sponges; in shallow depths.

Distribution. Japan, Western Mediterranean, USA (Massachusetts), Australia (New South Wales, Tasmania, Western Australia).

Syllides pumilus Hartmann-Schröder, 1983

Fig. 88A–F

Syllides articulosus pumilus Hartmann-Schröder, 1983: 131, figs 16, 17; 1984: 21; 1986: 42; 1987: 38; 1989: 26.

Material examined. AUSTRALIA: NEW SOUTH WALES: S of airport runway extension, Botany Bay, 33°58.13'S 151°11.16'E, 5 m, coll. Australian Museum party, 6 Apr 1992, 1 (AM W23118); Currambene Creek, Jervis Bay, 35°02'S 150°40'E, intertidal unvegetated sediment, coll. L. Howitt, Dec 1988, 1 (AM W22608). WESTERN AUSTRALIA: Dunsborough, 33°36'S 115°06'E, *Posidonia* & *Halophila* seagrasses, intertidal, coll. G. Hartmann-Schröder, 9 Nov 1975, 2 paratypes (AM W196214); reef W of Groyne, 2 km S of Cape Peron, 32°16'S 115°41'E, orange sponge in deep channel in limestone reef, 4.5 m, coll. R.T. Springthorpe, 26 Dec 1984, 1 (AM W28367); Limestone reef, off Ned's camp, Cape Range National Park, 21°59'S 113°55'E, sponge with epiphytic algae, & muddy worm tubes, 1.5 m, coll. R.T. Springthorpe, 2 Jan 1984, 1 (AM W27652).

Description. Body 2.4 mm long, 0.2 mm wide, with 30 chaetigers, dorsum with bright, minute inclusions, density of inclusions varies between individuals, fragile, most appendages missing on all specimens. Prostomium oval, with 4 eyes arranged in open trapezoidal pattern, and 2

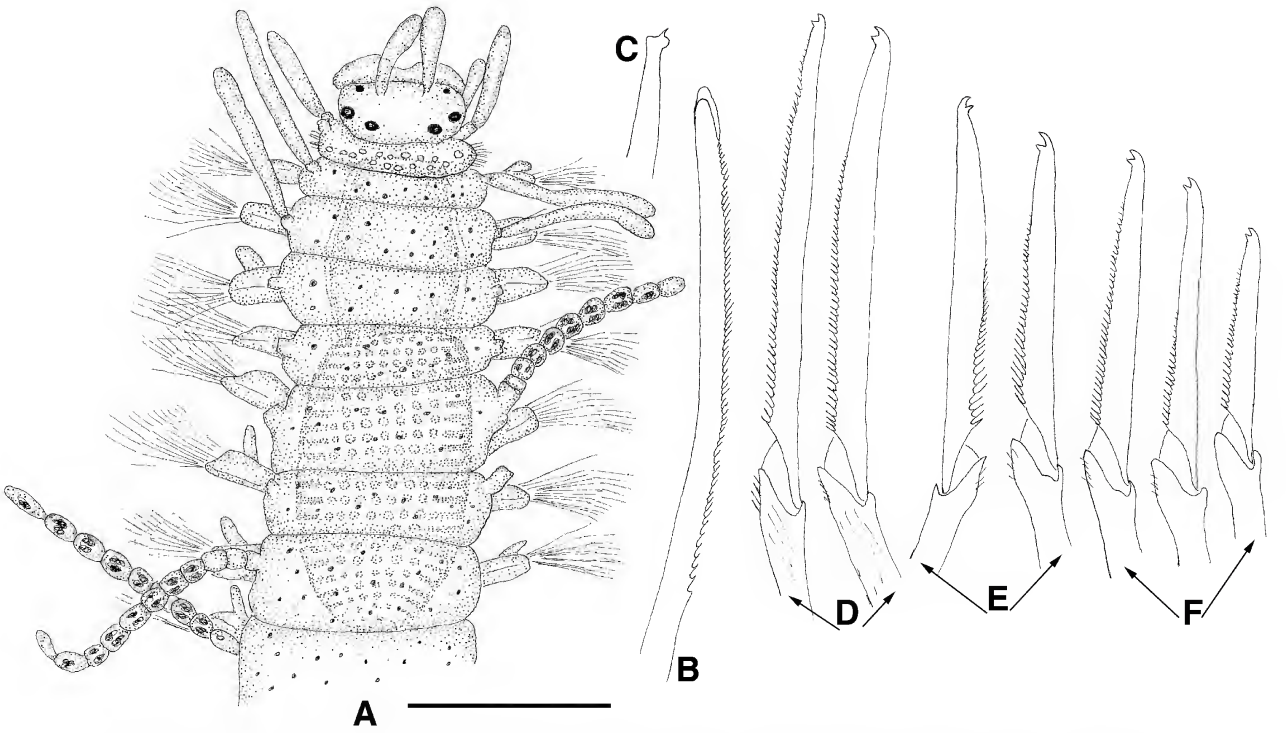


Fig. 88. *Syllides pumilus* Hartmann-Schröder, 1983 (*A*) anterior end, dorsal view; (*B*) dorsal simple chaeta; (*C*) acicula; (*D*) dorsalmost pair of compound chaetae; (*E*) second pair of compound chaetae; (*F*) compound chaetae of remaining pairs, midbody parapodium. AM W26322. Scales: *A* 0.18 mm, *B–F* 20 µm.

anterior eyespots; 3 antennae all similar. Palps basally fused, shorter than prostomium (Fig. 88A). Peristomium with hyaline inclusions, larger than inclusions on dorsum; tentacular cirri elongated, slightly club-shaped, longer than lateral antennae (Fig. 88A), ventral tentacular cirri about two thirds length of dorsal cirri. Dorsal cirri of chaetigers 1, 2, elongated, longer than tentacular cirri, similar in length to body width; from chaetiger 3 onwards, dorsal cirri articulated (Fig. 88A), with about 10 articles (up to 16, fide Hartmann-Schröder), cirri mostly broken, articles usually with 1–2 dark, granular inclusions. Parapodia trapezoidal dorsally, slightly larger on anterior parapodia, becoming conical and slender from mid parapodia onwards. Ventral cirri digitiform, similar in length or shorter than parapodial lobes. About 15 compound chaetae on anterior parapodia, numbers diminishing progressively along body to about 10; shafts with thin subdistal spines; blades elongated, bidentate, with short spines on margin, without basal spurs (Fig. 88D–F), with dorsoventral gradation in length of blades within fascicle, about 50 µm in length dorsally, 20 µm in length ventrally, on midbody. Dorsal simple chaetae from chaetiger 1, distally blunt, with small distal hood and short spines on margin (Fig. 88B). Ventral simple chaetae absent. All parapodia with single acicula, distally knobbed, with filiform, short tip (Fig. 88C). Pharynx through 4 segments. Proventricle through 4 segments (Fig. 88A), with 24–30 muscle cell rows.

Remarks. *Syllides articulosus* Ehlers, 1897, from Magellan Strait, in South America, appears to be a different species to the Australian specimens that were described by Hartmann-Schröder (1983) as a subspecies *Syllides articulosus pumilus*. *Syllides articulosus* has a proventricle distinctly longer than the pharynx (see Ehlers, 1897, pl. II, Fig. 52), and the dorsal simple chaetae are distally pointed, and lack a distal hood (Banse, 1972). We suggest that such differences are sufficient to warrant elevating the subspecies of Hartmann-Schröder to a full species *Syllides pumilus*. *Syllides bansei* Perkins, 1981, from Florida and the Mediterranean Sea, has similar dorsal simple chaetae, but the blades of the second pair of compound chaetae within each fascicle are provided with a long basal spur (see Perkins, 1981; San Martín, 2003).

Habitat. Occurring on sponges, algae, *Posidonia*, and in sediments, from intertidal to shallow depths.

Distribution. Australia (Western Australia, South Australia, Victoria, New South Wales).

Syllides spinosus Hartmann-Schröder, 1979

Fig. 89A–C

Syllides articulosus spinosus Hartmann-Schröder, 1979: 99, figs 126–128; 1981: 34; 1991: 37.

Material examined. AUSTRALIA: NEW SOUTH WALES: NE corner of Clark Is., 33°51.85'S 151°14.47'E, encrustation on outside of bottle, 5 m, coll. P.A. Hutchings, 17 Apr 1996, 2 (AM W26322). WESTERN AUSTRALIA: Exmouth, Tantabiddy Creek, 21.56°S 113°58'E, medium sand, intertidal, coll. G. Hartmann-Schröder, 1 (HZM P-16907).

Description. Body 2.2 mm long, 0.3 wide mm with 30 chaetigers. Dorsal cirri long, with hyaline vacuoles on most articles (Fig. 89A). Tufts of cilia in front of each anterior eyespot. Ciliary bands on dorsum of each segment (Fig. 89A). Parapodia with about 5 compound chaetae, relatively long blades, bidentate, both teeth distinctly separated, with short spines on margin; blades of 2 medium length

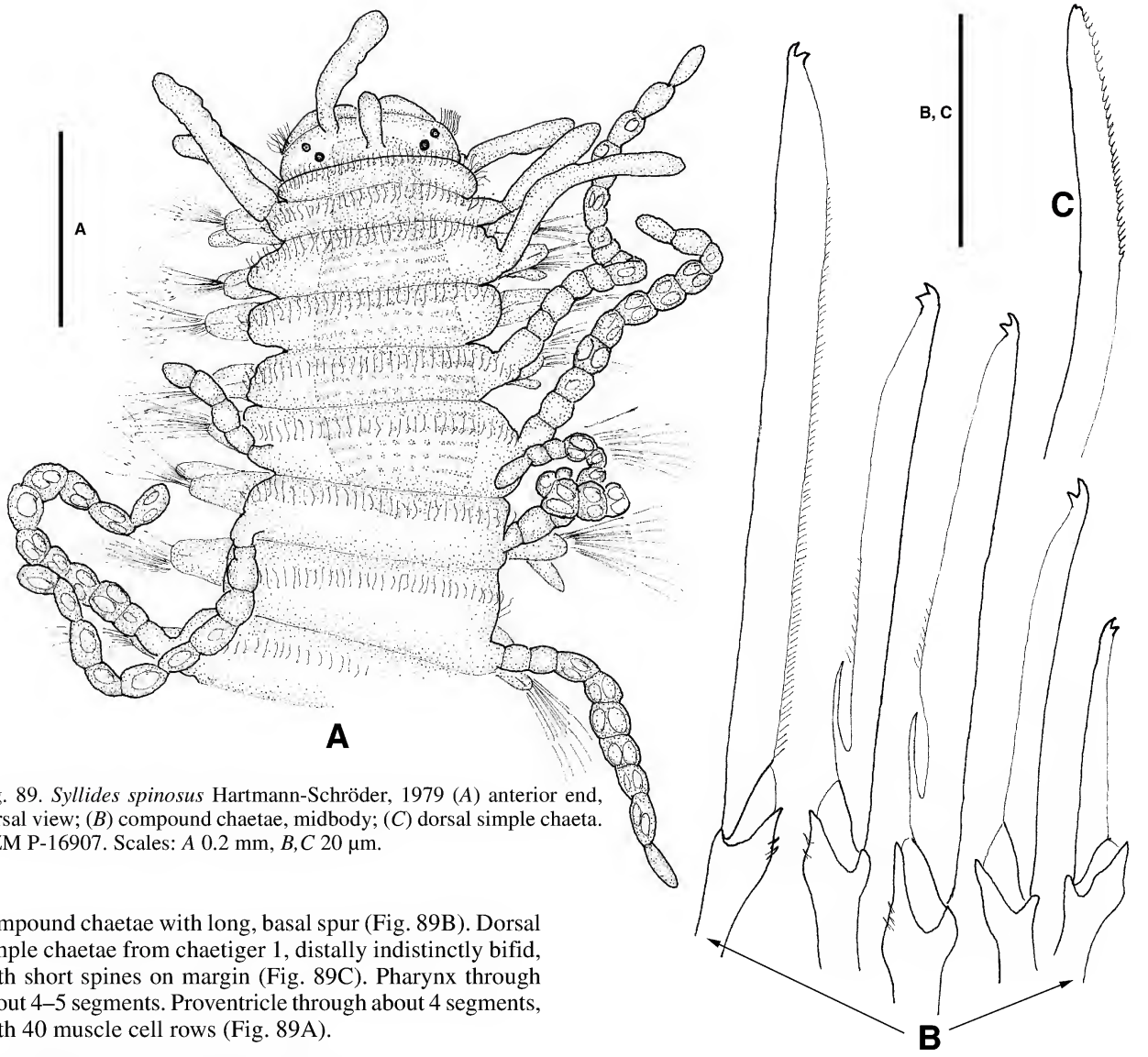


Fig. 89. *Syllides spinosus* Hartmann-Schröder, 1979 (*A*) anterior end, dorsal view; (*B*) compound chaetae, midbody; (*C*) dorsal simple chaeta. HZM P-16907. Scales: *A* 0.2 mm, *B,C* 20 µm.

compound chaetae with long, basal spur (Fig. 89B). Dorsal simple chaetae from chaetiger 1, distally indistinctly bifid, with short spines on margin (Fig. 89C). Pharynx through about 4–5 segments. Proventricle through about 4 segments, with 40 muscle cell rows (Fig. 89A).

Remarks. The long, basal spurs on medium-length blades of compound chaetae have not previously been described. This character is considered to be a useful character to distinguish between species in this genus. *Syllides bansei* Perkins, 1981, has similar compound chaetae, but the dorsal simple chaetae differ in having a distal hood (Perkins, 1981). *Syllides edentatus* Westheide, 1974, also has a similar arrangement of chaetae, but the pair of the medium size chaetae have several long spines instead of a single basal spur as occurs in *Syllides spinosus* (Westheide, 1974; San Martín, 2003). *Syllides benedicti* Banse, 1972, also has a single long basal spur on the pair of medium-length bladed chaetae, but the dorsal simple chaetae are distally rounded, with some spines present in addition to the spines on margin (Banse, 1972). For a discussion of the differences between the stem species *S. articulosus* and *S. spinosus* see Hartmann-Schröder, 1979; furthermore, *S. articulosus* lacks long basal spurs on any blade (Somaschini & San Martín, 1997).

Habitat. Occurring in coarse and medium sand, on encrustations, from intertidal to shallow depths.

Distribution. Australia (Western Australia, Victoria, South Australia, New South Wales).

Syllides tam n.sp.

Figs 86A,B, 90A–G

Syllides longocirrata.—Augener, 1913: 229.—Haswell, 1920: 102.—Hutchings & Murray, 1984: 33. Not Örsted, 1845: 11.

Material examined. HOLOTYPE (AM W28472) AUSTRALIA: NEW SOUTH WALES: 1.5 km SE of Dangar Is., Hawkesbury R., 33°33'S 151°14'E, sandy mud, 7 m, coll. Jones & party, 21 Aug 1980. PARATYPES. 50 m NE of Green Point, Hawkesbury R., 33°33.5'S 151°14.5'E, sandy mud, 4 m, coll. A.R. Jones & party, 17 May 1982, 1 (AM W24704); 300 m NE of Green Point, Hawkesbury R., 33°34'S 151°13.5'E, sandy mud, 5 m, coll. A.R. Jones & A. Murray, 18 Nov 1980, 1 (AM W28463); 1 km S of E end, Spectacle Is., Hawkesbury R., 33°32'S 151°07.5'E, muddy sand, 12 m, coll. A.R. Jones & A. Murray, 5 Aug 1983, 1 (AM W28464); 1 km S of E end, Spectacle Is., Hawkesbury R., 33°32'S 151°07.5'E, muddy sand, 12 m, coll. A.R. Jones & A. Murray, 11 Nov 1983, 1 (AM W28465); 1 km SE of Dangar Is., Hawkesbury R., 33°33'S 151°14'E, shelly mud, 9 m, coll. A.R. Jones & party, 1 Aug 1979, 1 (AM W28466); 1 km SE of Dangar Is., Hawkesbury R., 33°33'S 151°14'E, shelly mud, 9 m, coll. A.R. Jones & party, 21 Aug 1980, 1 (USNM 1082992); 30 m SE of Brooklyn boat-channel, Hawkesbury R., 33°33'S 151°14'E, shelly mud, 7 m, coll. A.R. Jones & party, 18 Dec 1979, 1 (LACM ex AM W28469); 30 m SE of Brooklyn boat-channel, Hawkesbury R., 33°33'S 151°14'E, shelly mud, 7 m, coll. A.R. Jones & party, 1 Aug 1979, 1 (AM W28470); 1.5 km SE of Dangar Is., Hawkesbury R., 33°33'S 151°14'E, sandy mud, 7 m, coll. A.R. Jones & party, 1 Aug

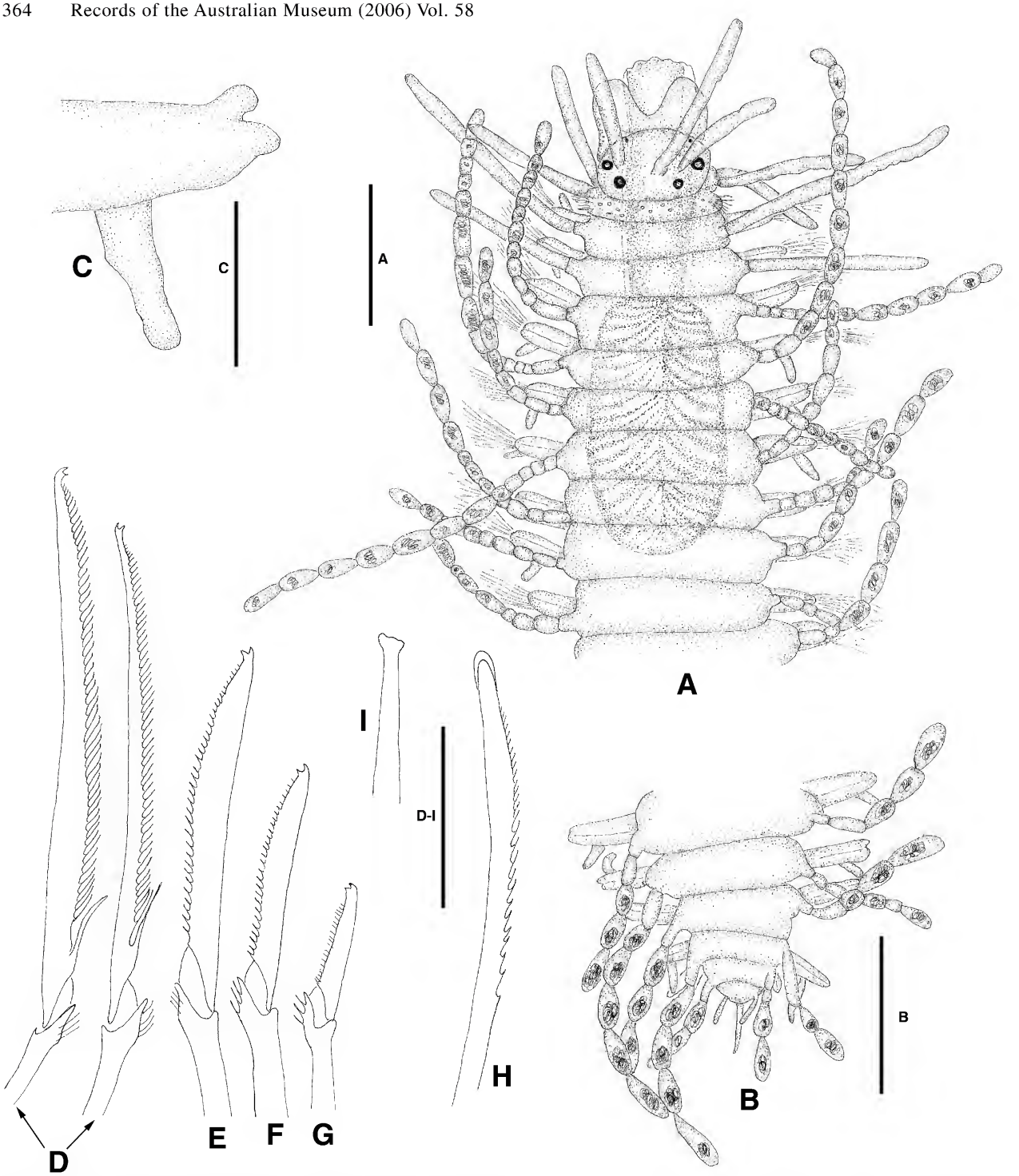


Fig. 90. *Syllides tam* n.sp. (*A*) anterior end, dorsal view; (*B*) posterior end, dorsal view; (*C*) parapodial lobe; (*D*) compound chaetae of longest and second pair, midbody parapodium; (*E*) compound chaeta of third pair; (*F*) compound chaeta of fourth pair; (*G*) compound chaeta of fifth pair; (*H*) dorsal simple chaeta; (*I*) acicula. AM W28472. Scales: *A,B* 0.1 mm; *C* 37 µm; *D–I* 20 µm.

1979, 3 (AM W28471); 1.5 km SE of Dangar Is., Hawkesbury R., 33°33'S 151°14'E, sandy mud, 7 m, coll. A.R. Jones & party, 18 Dec 1979, 1 (AM W28473); Brooklyn boat-channel, Hawkesbury R., 33°33'S 151°14'E, fine mud, 3 m, coll. A.R. Jones, 16 May 1980, 1 (AM W28474); Midway between Green Point and Croppy Point, Hawkesbury R., 33°33.5'S 151°14.5'E, mud, 6 m, coll. A. Jones & party, 22 Nov 1980, 1 (AM W196517); E end Brooklyn boat channel, 1 (AM W196518); Liverpool Reach, Hawkesbury R., 33°25'S 150°56'E, fine sand, 4 m, coll. A. Jones & party, 21 Feb 1980, 1 (AM W196657); Liverpool Reach, Hawkesbury R., 33°25'S 150°56'E, coarse sand, 20 m, coll. A. Jones & party, 21 Feb 1980, 3 (AM W196658); Liverpool Reach, Hawkesbury R., 33°25'S 150°56'E, coarse sand, 20 m, coll. A. Jones & party, 21 Feb 1980, 21 (AM W196659).

Additional material examined. QUEENSLAND: At mouth of Althaus Creek, Halifax Bay, 19°10'S 146°36'E, 2 m, coll. Queensland Nickel, Jan 1977, 2 (AM W28207). NEW SOUTH WALES: 0.5 km E. of Dangar Is., Hawkesbury R., 33°33'S 150°14'E, coll. A. Jones & party, 21 Aug 1980, 4 on SEM stub (AM W196520); S of airport runway extension, Botany Bay, 33°58.13'S 151°11.16'E, 5 m, coll. Australian Museum party, 7 Apr 1992, 1 (AM W21631); SW of airport runway extension, Botany Bay, 33°58.33'S 151°10.22'E, 7 m, coll. Australian Museum party, 28 July 1992, 1 (AM W21632); E of Marley, 34°08.08'S 151°09.65'E, sand, 60 m, coll. Fisheries Research Institute (NSW), 2 May 1991, 1 (AM W24377); Bass Point, 34°36'S 150°54'E, 50 m, coll. The Ecology Lab for RMI/Pioneer Project, 1 Feb 1990, few (AM

W22994); Montagu Roadstead, Jervis Bay, 35°02.2'S 150°46'E, 12 m, coll. P.A. Hutchings & party, 6 Jun 1991, 1 (AM W27574). VICTORIA: Port Phillip Bay, 38°09.3'S 144°42.7'E, sand, 3 m, coll. Marine Pollution Studies Group, 11 Jun 1971, 2 (AM W16236).

Description. Body about 2.4 mm long, 0.2 mm wide, with 30 chaetigers. Prostomium oval, slightly wider than long; 4 eyes arranged in open trapezoidal pattern and 2 anterior eyespots; median antenna inserted between posterior eyes, about one and half times combined length of prostomium and palps, lateral antennae about two thirds of length of median antenna, inserted near anterior eyes (Fig. 90A). Palps similar in length to prostomium, without distal papillae. Peristomium slightly shorter than subsequent segments, with hyaline, rounded inclusions; dorsal tentacular cirri similar to median antenna, slightly shorter; ventral tentacular cirri about two thirds length of dorsal ones (Fig. 90A). Antennae, tentacular, and dorsal cirri of chaetigers 1 and 2, elongate, slender; dorsal cirri of chaetiger 1 longer than median antenna, those of chaetiger 2 shorter than those of chaetiger 1, similar in length to median antenna. Dorsal cirri of subsequent segments alternating irregularly with long cirri, distinctly longer than body width, with about 10–12 articles; short cirri, similar in length to body width, with about 6–7 articles; articles pyriform, usually with 1 dark inclusion (Fig. 90A). Parapodial lobes elongated, conical, distally bilobed (Fig. 90C). Ventral cirri digitiform, similar in length to parapodial lobes. Compound chaetae similar throughout, shafts with several, long, fine, subdistal spines, and elongated, bidentate blades, within fascicle 5 pairs of chaetae, each pair similar in shape and length (Fig. 90D–G). Blades of most dorsal pair of compound chaetae with single long, distinct basal spur, and moderate, thin spines on margin, about 60–62 μm long; blades of second pair similar to those of most dorsal pair, but shorter, about 52 μm long, with shorter spines on margin (Figs 90D, 86A). Blades of subsequent pairs without basal spur and having short spines on margin (Fig. 90E–G), 40, 27 and 15 μm in length respectively. Dorsal simple chaetae from chaetiger 1, unidentate, distally blunt, provided with distal hood and short spines on margin (under light microscope) (Fig. 90H); under SEM, hood consists of several rows of minute spines (Fig. 86B). Ventral simple chaetae absent. Acicula solitary, distally knobbed (Fig. 90I). Pharynx through 5–6 segments (Fig. 83A). Proventricle barrel-shaped, through about 5–6 segments, with 35 muscle cell rows. Pygidium small, semi-circular, with 2 short, smooth lateral anal cirri and 1 median, longer cirrus (Fig. 90B).

Remarks. This species has been reported in Australia as *Syllides longocirrata* (Örsted, 1845), which only occurs in the Northern Atlantic and Northern Pacific areas, and differs from the Australian specimens, which are described as a new species. *Syllides longocirrata* has dorsal simple chaetae that are pointed and without a hood, and the compound chaetae are unidentate (see Banse, 1972), whereas the compound chaetae of *Syllides tam* are distally blunt and hooded. *Syllides japonicus* Imajima, 1966 (see below) and *S. floridanus* Perkins, 1981, also have dorsal simple chaetae that are pointed, and without a hood (Perkins, 1981), which differ from those present in *Syllides tam*.

Habitat. Occurring in coarse, medium to muddy sand; from intertidal to 60 m.

Distribution. Australia (Queensland, New South Wales, Victoria).

Etymology. The species is named after The Australian Museum.

Syllides sp.

Fig. 91A–D

Material examined. AUSTRALIA: WESTERN AUSTRALIA: N end of beach, Bundegi Reef, Exmouth Gulf, 21°49'S 114°11'E, rocky rubble & sticky sediment with brown & epiphytic algae, 2 m, coll. H.E. Stoddart, 4 Jan 1984 (AM W28920).

Description. Body 2.0 mm long, 0.2 mm wide, with 25 chaetigers. Dorsum of each segment with 2–4 transverse rows, more or less well defined, of small, golden inclusions (Fig. 91A). Prostomium trapezoidal, with 2 distinct tufts of long cilia on anterior corners, and 4 eyes in open trapezoidal arrangement (Fig. 91A); antennae detached. Palps slightly shorter than prostomium. Peristomium similar in length to following segments, tentacular cirri missing. Dorsal cirri of chaetigers 1 and 2 smooth, elongated, longer than body width; remaining dorsal cirri articulated, long, up to 11 articles, with 1 dark inclusion of granular material in most articles (Fig. 91A). Compound chaetae with translucent hooded shafts serrated on edge, and relatively short, bidentate blades, with short spines on margin, and distributed in 5 pairs within fascicle, each pair of similar length (Fig. 91B); dorsal most pair 26 μm in length and ventral most pair 15 μm in length. Dorsal simple chaetae from chaetiger 1, slender, slightly bifid, with short spines on margin, lacking distal hood (Fig. 91C). Acicula solitary, distally knobbed, with distal, filiform tip (Fig. 91D). Pharynx long and slender, through 5 segments. Proventricle short, slender, through 2 segments (Fig. 91A), with about 17 muscle cell rows.

Remarks. This specimen is characterized by having a hood on the edge of shafts of compound chaetae, and blades lacking spurs. The most similar species is *Syllides gomezi* San Martín, 1990, from Cuba (San Martín, 1990). The Cuban species, however has a longer proventriculus through 4 segments, instead of through 2 as occurs in *Syllides* sp., and the dorsal simple chaetae are entire, distally pointed, whereas they are bifid in the Australian species. Other species of *Syllides* also lack basal spurs on the blades of compound chaetae, but none have a hood on the edge of shafts. *Syllides sanyaensis* Ding & Westheide (1997) described from China, is similar, but the dorsal simple chaetae are hooded whereas those of this specimen lack such hoods. Since we have a single, somewhat damaged specimen, we prefer not to describe this species as a new species.

Habitat. Rocky rubble and sediment with brown and epiphytic algae, in depths of 2 m.

Distribution. Australia (Western Australia).

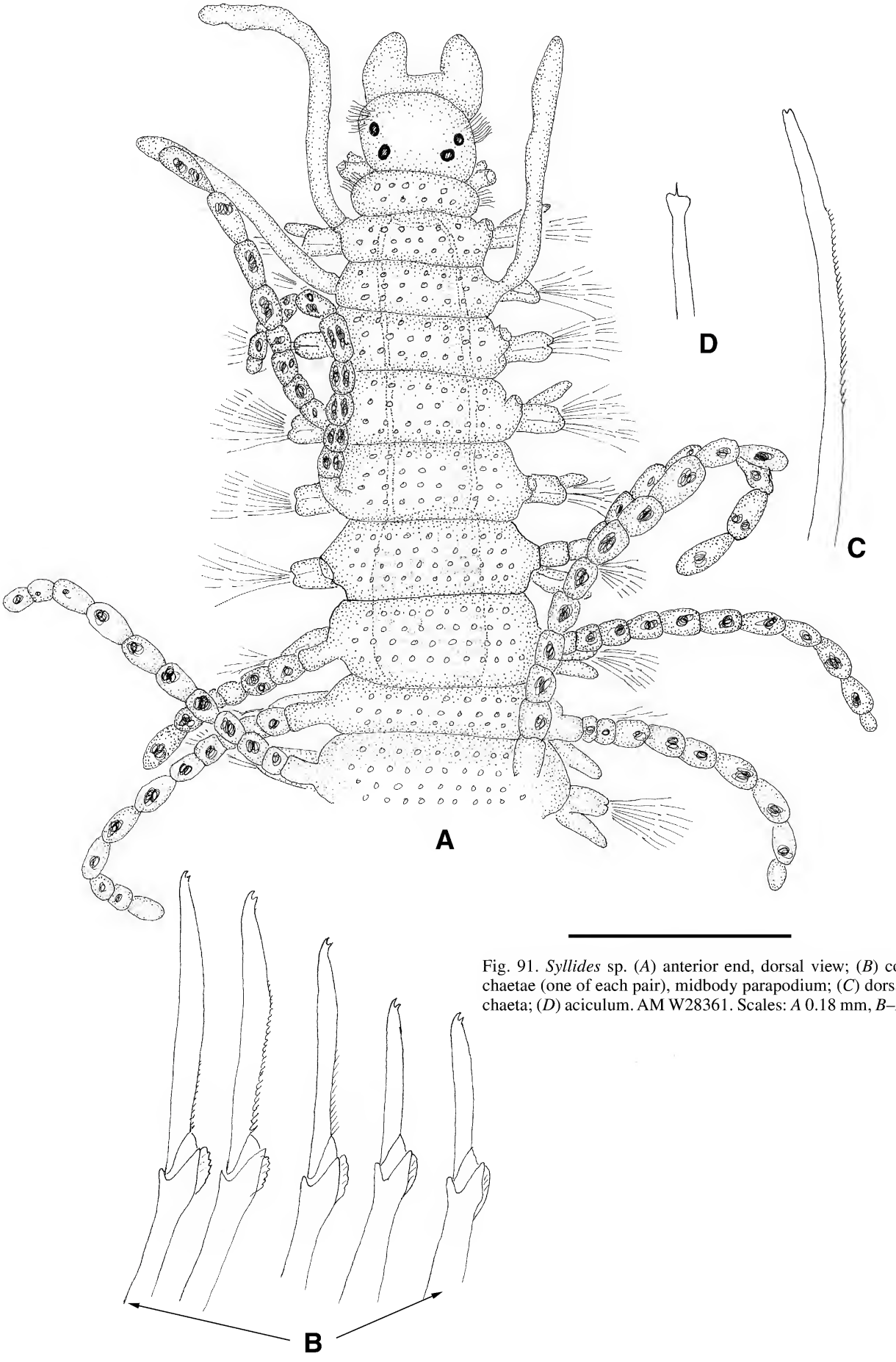


Fig. 91. *Syllides* sp. (*A*) anterior end, dorsal view; (*B*) compound chaetae (one of each pair), midbody parapodium; (*C*) dorsal simple chaeta; (*D*) aciculum. AM W28361. Scales: *A* 0.18 mm, *B–D* 20 µm.

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Characterizing Late Pleistocene and Holocene Stone Artefact Assemblages from Puritjarra Rock Shelter: A Long Sequence from the Australian Desert

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ABSTRACT. This paper presents the first detailed study of a large assemblage of late Pleistocene artefacts from the central desert. Analysis of the lithics shows show that Puritjarra rock shelter was used more intensively over time, with significant shifts in the character of occupation at 18,000, 7,500 and 800 B.P., reflecting significant re-organization of activities across the landscape. The same generalized flake and core technology appears to have been used for over 30 millennia with only limited change in artefact typology over this period.

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Excavations at Puritjarra rock shelter provide a rare opportunity to examine an assemblage of late Pleistocene artefacts from central Australia, dating as early as c. 32,000 B.P. This study presents a quantitative analysis of the flaked stone artefacts at Puritjarra, comparing the Pleistocene and Holocene assemblages at this site. It is also the first detailed study of an excavated assemblage of lithics in the Australian arid zone since research by R.A. Gould on the Holocene artefact assemblages at Puntutjarpa (Gould, 1977) and Intirtekwerle (James Range East) (Gould, 1978), and R.J. Lampert at Hawker Lagoon (Lampert & Hughes, 1988). However, it differs from these earlier studies in making the history of site use a focus of analysis, rather than stone tool systematics.

This approach reflects current trends in lithic research. Over the last thirty years, interpretation of flaked stone artefact assemblages in Australia has swung from stone tool systematics to a more systemic perspective on stone artefacts (Holdaway & Stern, 2004—see also Cundy, 1990; Hiscock & Allen, 2000; Hiscock & Attenbrow, 2003; Holdaway, 2004). Ethno-archaeological studies involving the last generation of Aboriginal people to rely on stone artefacts have been very influential in this shift in perspective (Cane, 1984, 1992; Gould, 1968; Gould *et al.*, 1971; Hayden, 1977, 1979; O'Connell, 1977). But Australian research also reflects the impact of international trends in lithic analysis, stimulated by the work of L.R. Binford on site use, mobility patterning and organizational variability amongst foraging peoples (Binford, 1982). Recent research in the Australian arid zone emphasizes the effects of residential mobility, access to stone, the flaking properties of different raw materials, and changes in intensity of occupation as key factors in structuring the archaeological record (Barton, 2003; Veth, 1993).

Research problems in central Australia

The need for an extended application of this approach, to excavated assemblages of flaked stone artefacts from the western and central desert, has grown steadily since the prehistory of these regions was mapped out in a series of

regional studies in the 1980s and 1990s (Smith, 1988; Thorley, 1998b; Veth, 1989a). Some site use issues that now warrant more detailed analysis of flaked stone assemblages include:

The nature of late Pleistocene occupation. Late Pleistocene groups in the Western Desert and central Australia appear to have been small, highly mobile groups using wider territories than those in the Holocene (O'Connor *et al.*, 1998: 21; Smith, 1989, Smith *et al.*, 1998; Thorley, 1998b: 316). Preliminary analysis of changes in residential mobility, using a range of archaeological indices (including extent of stone reduction and artefact diversity), at the three known late Pleistocene sites in the region—Kulpi Mara, Puritjarra and Serpent's Glen—supports this proposition (Veth, 2005a) but detailed analysis of flaked stone assemblages is required to test it.

Impact of the last glacial maximum. Increasing aridity around 18,000–20,000 B.P. is thought to have led to changes in residential mobility, territory and regional networks (Smith, 1989, Smith *et al.*, 1998; Veth, 1989b, 1993, 2005b). Both Kulpi Mara and Serpent's Glen were abandoned after about 23,000 B.P. Only Puritjarra, near reliable water, shows evidence for use between 23,000 and 13,000 B.P., raising questions about the pattern of occupation at this time. Both Smith (1989) and Thorley (1998a: 43) argue that Puritjarra should show evidence of more intensive "water-tethered" occupation, with Smith opting for a "point-to-point" rather than a "home range" pattern of mobility (Smith, 1989).

Holocene shifts in mobility patterns. Thorley (1998b, 1999) shows there was widespread occupation of the upper reaches of the Palmer River catchment at 3,000–4,000 B.P., suggesting increased residential mobility and greater use of ephemeral waters. Hiscock (1994) suggests that the appearance of new toolkits around 4,000 B.P. represents a technological response to increased mobility, driven in part by greater environmental variability associated with ENSO. Although data on the mid-Holocene (4,000–6,000 B.P.) is comparatively poor for the western and central desert, analysis of excavated assemblages from Puritjarra and Serpent's Glen can test whether there are significant changes in site use at this time.

Late Holocene intensification. The last millennium appears to have been a period of major change in the Western Desert and central Australia (Smith, 1996; Thorley, 1999; Veth, 1993, 2005b), possibly involving shifts towards higher regional populations. There are indications of more intensive occupation and significant increases in the level of site use after 1,500–1,000 B.P.—especially in the lower reaches of catchments, in sites on sand plain and valley floors (Smith, 1988, 1996; Thorley, 1998b: chapter 8). The most pressing need is to "unpack" this phase of occupation and determine whether it reflects changes in the duration of visits (more sedentary occupation), changes in group size, or changes in the frequency of visits (more frequent cycling of groups through these sites). Both Behr (1990) and Law (2003) have suggested that increased mobility is involved in these changes, although both studies were limited (Behr looked mainly at cores; Law focussed only on retouched flakes).

Aim of this study

My aim is to provide a quantitative analysis of the flaked stone artefacts from Puritjarra in sufficient detail to characterize lithic assemblages from different phases of occupation of the shelter. This will provide the basis for reconstructing the history of use of the shelter and its place within a changing cultural landscape—and for testing ideas about mobility, site territory, and site use outlined above. There are limits to what can be inferred from a single site. However, this analysis of the Puritjarra assemblages should provide the basis for comparison with Kulpi Mara and Serpent's Glen, when quantitative data on their flaked stone assemblages becomes available.

This study is not primarily a technological or typological study but rather history-in-a-locale—or as L.R. Binford termed it an "archaeology of place" (Binford, 1982). It provides a historical portrait of a key desert site, complementing other studies which deal with the ^{14}C and luminescence chronology of the site (Smith *et al.*, 1997; Smith *et al.*, 2001), as well as its environmental evidence and sedimentary history (Bowdery, 1995, 1998; Smith *et al.*, 1995), flaked stone artefacts (Behr, 1990; Law, 2003), grindstones and plant use (Smith, 2004), rock-art (Rosenfeld & Smith, 2002; Ross, 2003), ochres (Smith *et al.*, 1998), and Aboriginal history of the rock shelter (Smith, 2005a).

Background

Environmental setting. The western part of central Australia contains a diversity of country, including sand plain, dune fields, stony desert, salt lakes and rock outcrops. Scattered across the dominant sand hill and spinifex country, is an archipelago of small rocky ranges, often only a few kilometres long, and visible one from another on the horizon. Puritjarra is situated in the Cleland Hills (23°50'S 130°51'E), one of these small range systems, 60 km west of the MacDonnell Ranges (Fig. 1). The area is a transitional zone between ranges and desert lowlands: it shares the ecological and biogeographical features of country further west but is within a few days walk of the main central Australian range system.

Palaeoenvironments. Direct palaeoenvironmental evidence for the region is sparse (but see Bowdery, 1995, 1998; Hesse *et al.*, 2004, 2005; Smith *et al.*, 1995). Available data suggests an open local vegetation during much of the late Pleistocene, with scattered trees and sand hill shrubs but little grass cover—especially during the peak of the last glacial maximum around 18,000 B.P. Phytolith data and charcoals from the Puritjarra sediments indicate that the post-glacial period in central Australia saw a rapid amelioration of arid conditions with an increase in grasses and acacias by 13,000 B.P. The early Holocene vegetation may have been a mosaic of acacia woodland and spinifex communities, reflecting better rainfall at this time. Megirian *et al.* (2002) report that the early Holocene fauna included a wide range of macropods, as well as hairy-nosed wombat (*Lasiorhinus* cf. *latifrons*) and Tasmanian Devil (*Sarcophilus harrisii*), both of which became regionally extinct in the mid-Holocene. The mid-Holocene saw a decline in grass levels after 5,000 B.P., possibly in response to increasing aridity, which only recovered again after about 1,500 B.P. as the modern vegetation took shape. Assuming that periods

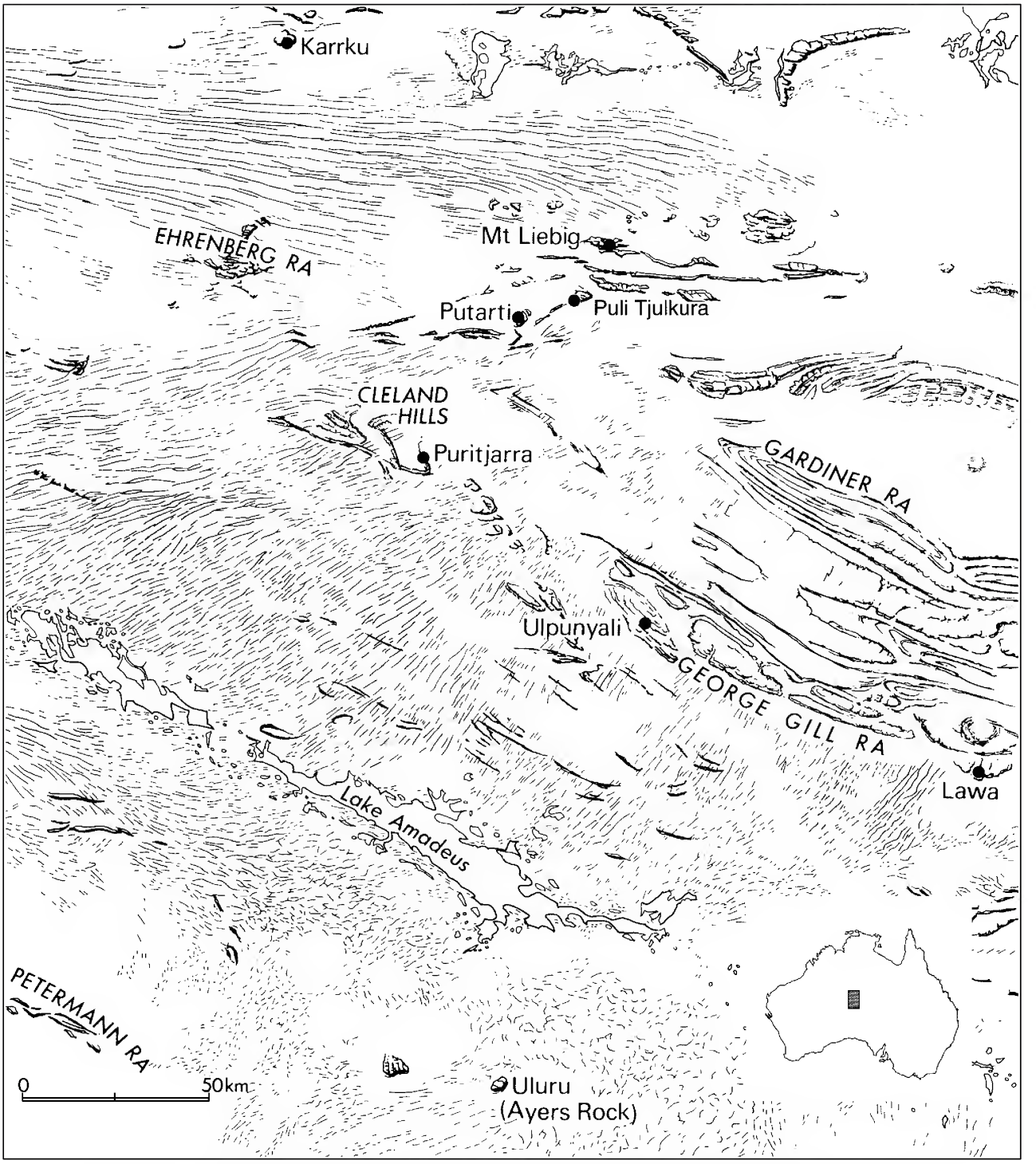

Fig. 1. The western part of central Australia showing the location of Puritjarra rock shelter and regional topography of longitudinal dunes, sandstone ridges and salt lakes.

of high representation of Poaceae in the phytolith record reflect better summer rainfall (which is likely), the last millennium was the most favourable period for human settlement in Central Australia during the last 50,000 years (Bowdery, 1995: fig. 6.1).

Puritjarra rock shelter

The rock shelter is situated at the foot of a small (15 m high) sandstone escarpment and faces out onto sand plain and dune field supporting spinifex hummock grassland and low shrubs. Behind and above the shelter there is an extensive low sandstone plateau with an open shrub cover of cypress pine (*Callitris glaucophylla*) and hill mulga (*Acacia macdonnelliensis*). There is a small ephemeral rock hole adjacent to the site. Reliable water is available at Murantji rock hole, a large semi-permanent (possibly spring-fed) rock hole c. 2 km north of the rock shelter. Morphologically, the site is a large open rock shelter formed in Ordovician-Devonian Mereenie sandstone, with a level sandy floor of c. 400 m^2 (Fig. 2). Floor to ceiling height is c. 12 m across much of the site.

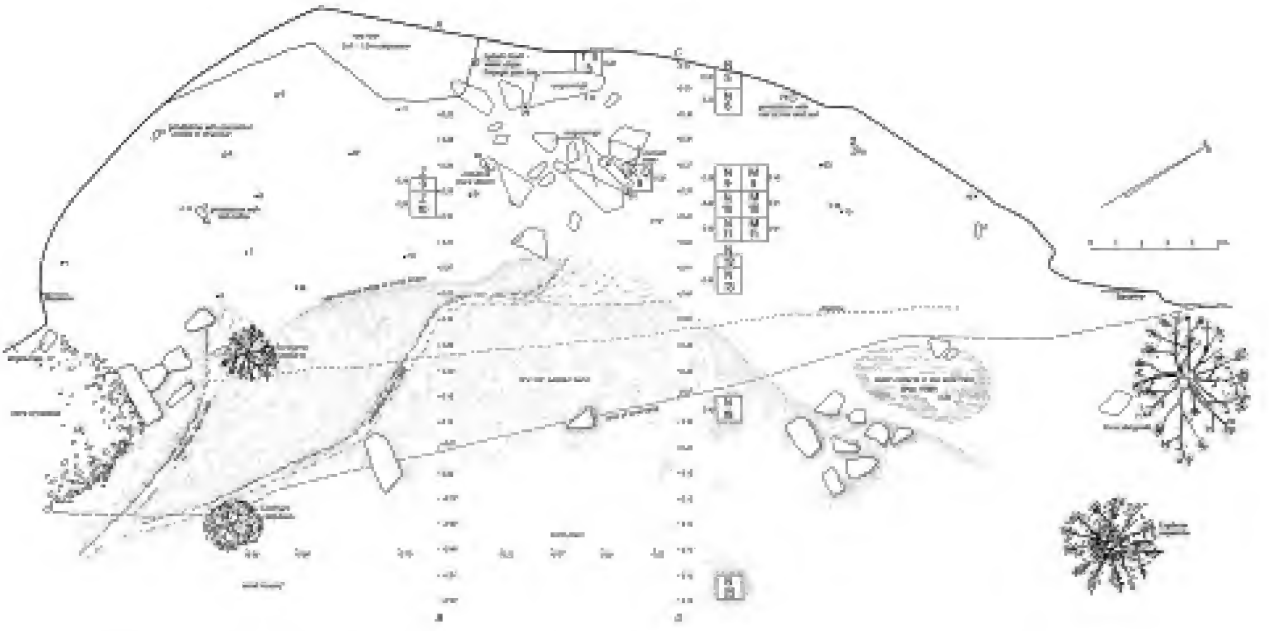

Fig. 2. Plan of Puritjarra rock shelter showing layout of excavation trenches. Also shown are spot heights (m below datum) for the ground surface.

Rock art. The rock art is described elsewhere by Rosenfeld & Smith (2002) and Ross (2003). A small number of rock engravings, mainly plain pecked circles, and incised lines occur on boulders embedded in the floor of the shelter (Fig. 2). Radiocarbon dates for the sedimentary surface these rest on, together with estimates of the age of the patina covering the engravings, suggest the pecked circles date between 13,500 and 7,500 B.P. (Rosenfeld & Smith, 2002:117). The rear wall of the rock shelter also forms a large painted frieze, 2 m high and c. 40 m long, containing more than 400 individual paintings, prints or stencils, most of which appear to have been produced during the last millennium.

Excavations 1986–1990

Three seasons of archaeological excavations were undertaken at the site between 1986 and 1990. The excavations, which are large by contemporary Australian standards, were intended to sample the shelter floor and stratigraphy across the site, and to explore the changing spatial structure of occupation within the rock shelter (Fig. 2). Given the paucity of knowledge about late Pleistocene and early Holocene occupation in the arid zone, I also aimed to recover an assemblage of artefacts large enough to support a quantitative analysis. Excavation trenches were positioned to sample the major discard zones across the rock shelter, particularly areas where larger artefacts such as cores and grindstones might accumulate. The Main Trench was opened up in the northern sector of the site to allow access to the lower part of the stratigraphic column, where rock fall had blocked more limited trenching in 1986 (Smith, 1987), and to follow a discrete layer of artefacts and occupation debris (unit 2c below) that emerged during the 1988 field season.

Excavation units (spits) take into account sedimentary bedding, natural stratigraphy and occupation features (such as pits and hearths) and therefore vary from 20–100 mm in depth (20–30 mm for most spits in layer II) and up to 1 m^2 in plan. During excavation of the Main Trench in 1988 and 1990 (involving grid-squares N11–N13, M10–M11) an attempt was made to record all artefacts in layer II in-situ. The aim was establish whether excavating in 20–30 mm spits was obscuring finer pulses of occupation (The results show this was not the case—see Fig. 21). These "levelled" finds form 67% (N = 237) of the total artefacts recovered from these spits.

Individual spits and small finds are identified using a hierarchical system, which describes their provenance (following Johnson, 1979:154–155). For instance, M10/1-7 is: (grid square M10)/(spit 1)-(find number 7). Both spits and finds are numbered in sequence within individual grid squares. Following Johnson (1979), there is no direct correlation between co-numbered spits in different grid squares.

Chronology

The chronology for the site is provided by a series of 31 radiocarbon dates on charcoal (Smith *et al.*, 1997; Smith *et al.* 2001). Nine luminescence dates on sediments are also available for the site. Some radiocarbon anomalies noted in the 1997 study have been shown to be due to younger contaminants rather than displacement of charcoal (Smith *et al.*, 2001). Extensive work on the chronology of the site since the preliminary reports (Smith, 1987, 1989) shows that levels initially dated to 22,000 B.P. are much older: c. 32,000 B.P. (^{14}C) or 35,000 years ago (TL). Together with phytolith research by D. Bowdery (1995, 1998), this work more accurately identifies the level corresponding to the peak of the last glacial maximum at this site (at 105 cm below datum), and also provides a better age estimate for the base of unit 2a (see below).

Using the radiocarbon chronology the occupational history of the rock shelter can be briefly summarized as follows: the site was occupied by at least c. 32,000 B.P. and use of the shelter continued throughout the late Pleistocene; the level of occupation increased after c. 7,500 B.P., and again during the last millennium.

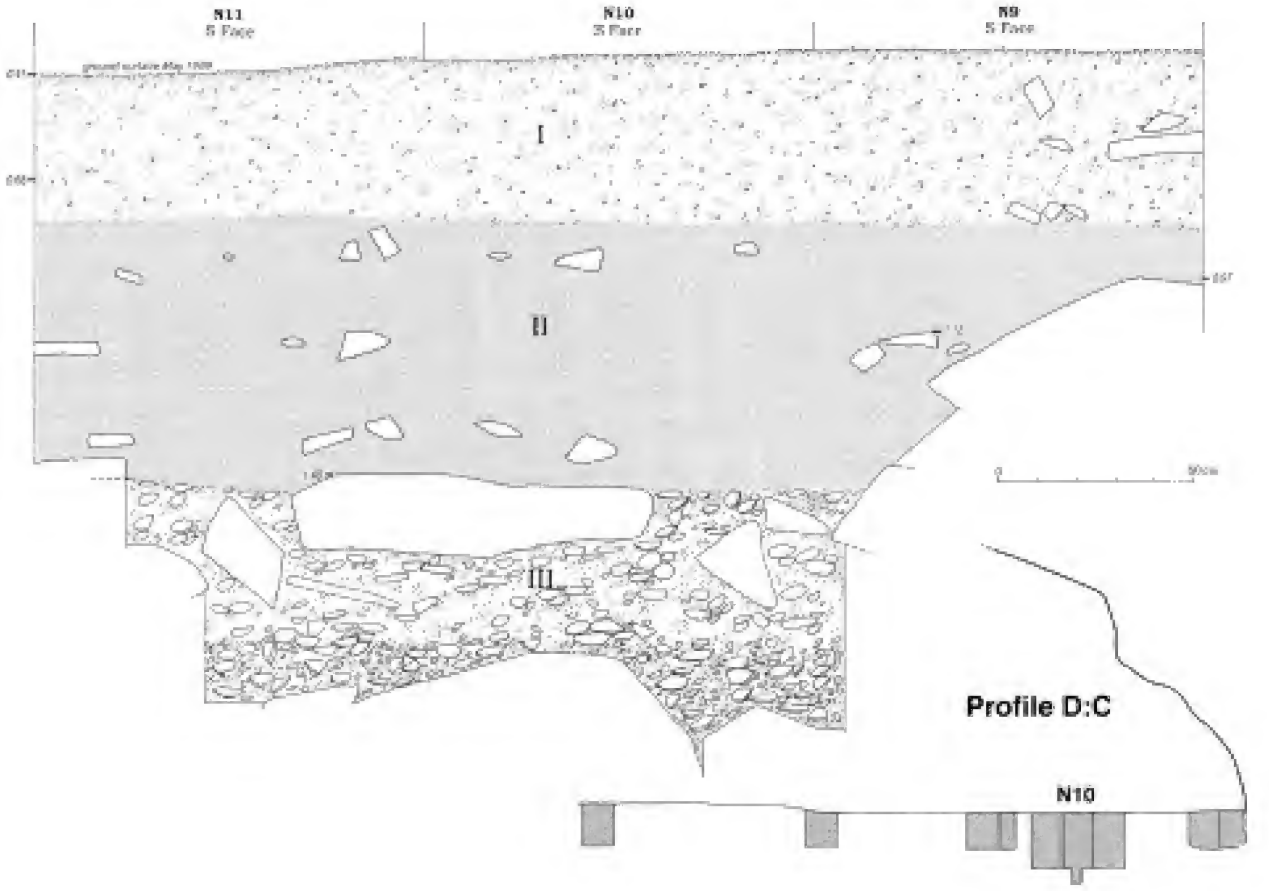

Fig. 3. Stratigraphic section, south face of the Main Trench, showing horizontal bedding of layers I–III. The inset provides a sagittal profile across the rock shelter.

Layers

The deposit, which is 2 m deep, is divisible into three major lithostratigraphic units (layers I to III) (Figs 3 and 4). These are more or less horizontally bedded and are made up of fine aeolian sediments, originating outside the shelter, together with varying size-grades of sandstone fragments derived from the shelter itself.

Layer III, consisting of rounded sandstone rubble, fine dark red sand, and large roof fall debris, is the oldest of these layers. It is at least 1.20 m thick but its full depth was not established. Luminescence dating (Smith *et al.*, 1997) indicates that the upper part of the layer dates to 96±7 ka (AdTL91011), suggesting a last interglacial age for much of the layer.

Layer II is a distinctive layer of hard, compacted, red silty sediment, about 60 cm thick. It rests unconformably on layer III. Both ^{14}C and luminescence dating techniques indicate the greater part of layer II is late Pleistocene in age, ranging in age from about 7,500 B.P. to 9,000 B.P. for the top of the layer to 44.8±3.6 ka (AdTL91010) at its base.

Layer I, which is about 42 cm thick, is a consolidated layer of fine, brown aeolian sand and rock spall, spanning the last 7,500 years. Its accumulation may represent more aggressive weathering of the roof of the shelter, initiated under the more humid conditions of the early Holocene.

Evidence for human occupation of the rock shelter is restricted to layers I and II. Apparent rates of sediment deposition at Puritjarra are low, averaging 23 mm per 1,000 yr (using the ^{14}C chronology), but are not unusual for Australian rock shelter deposits. Because of the increasing compaction with depth of sediments, these figures are likely to underestimate actual rates of sediment accumulation, especially for layer II.

The first people to visit Puritjarra would have found a rock shelter of similar size and morphology to that of the present day. The roof-fall debris in layer III represents the last major event to significantly alter the morphology of the rock shelter. Excavations in grid-square N18 revealed a column of rocks directly beneath the leading edge of the overhang, showing there has been little retreat of the shelter over the last 10,000 years. However, the available floor area appears to have changed over time. Initially the only large rock-free floor area was in the northern half of the shelter. As layer II built up it buried much of the rock fall and rubble in other parts of the shelter, extending the area available as a living surface.

Analytical units

Stratigraphic correlations between trenches are summarized in Fig. 4. The deposit can be divided into seven analytical units (units 1a–c within layer I, units 2a–d within layer II). Each represents an identifiable occupation horizon—which can be traced across the site—or parts of the deposit intercalated between these horizons. As these are divisions based on cultural stratigraphy, not arbitrary units, they do not necessarily represent equivalent blocks of time. Essentially, the analytical units represent the finest scale

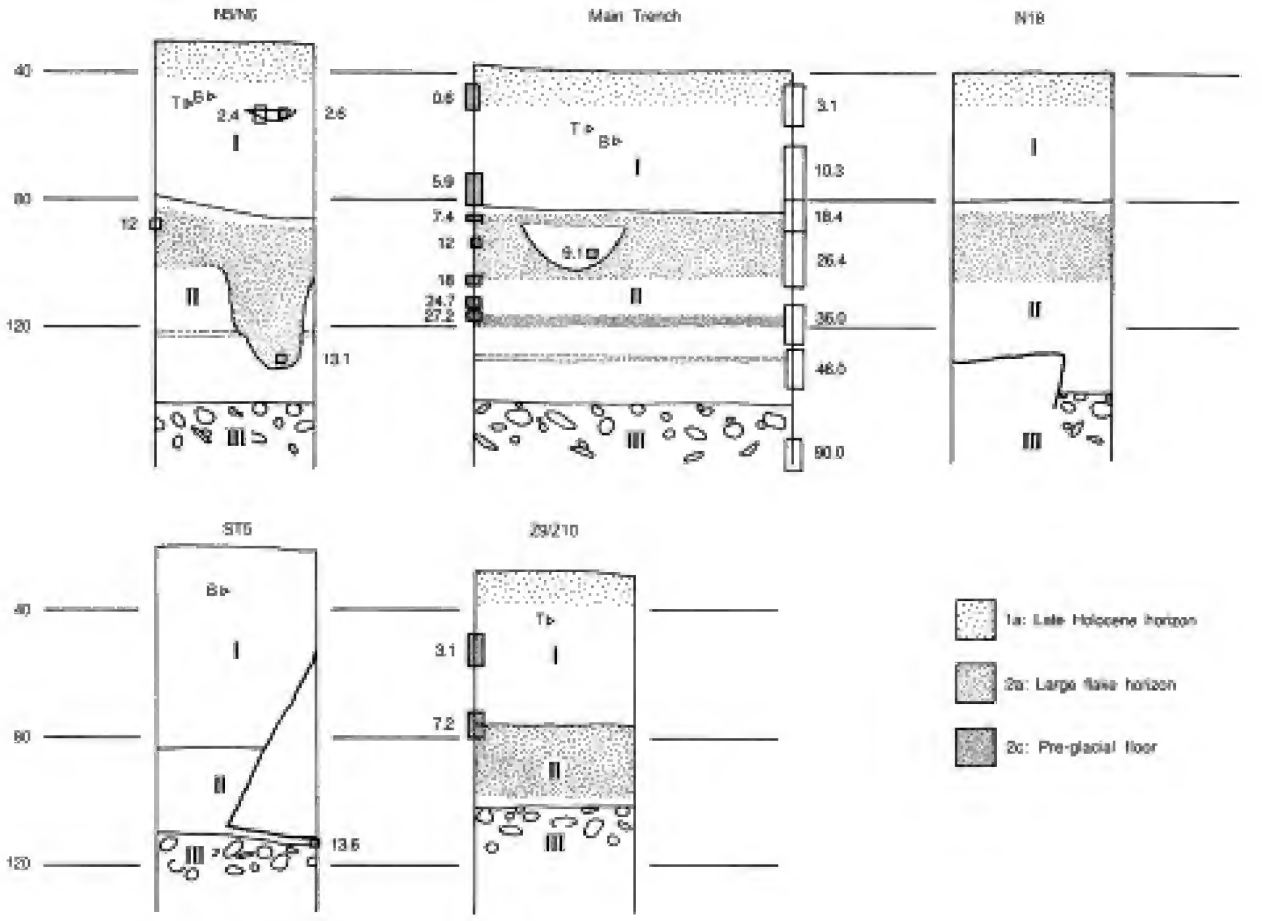

Fig. 4. Schematic diagram showing stratigraphic correlations between trenches. Layers I–III are labelled in bold. Identifiable cultural horizons (units 1a, 2a and 2c) are shown (stippled), as well as dated hearths (plano-convex features), ^{14}C determinations (hatched rectangles), luminescence dates (open rectangles) and the maximum depth of late Holocene artefacts in each trench (T tula adzes; B backed artefacts/geometric microliths). Grid lines show depth (cm) below site datum. Horizontal stippled lines at 120 cm depth in N5/N6 and in the Main Trench show the position of a silty band identified in grain-size analyses.

Table 1. Correlation of layers, analytical units and cultural horizons.

layer	unit	estimated age years B.P.	cultural horizon	indicative depth* (cm) below datum	below surface	related features
I	1a	0–800	Late Holocene zone of intensive occupation	40–50	0–10	*Hearths and ash lenses*: N5/2-1, N6/3-1, N6/4-1, N10/2, N11/3-4, M10/3-1, M9/2-1, M9/2-2, Z9/2, Z9/3. *Pits*: N12/3, N12/2-1, N25
I	1b	800–3,500		50–70	10–30	*Hearths and ash lenses*: N5/5-3, N6/7-2
I	1c	3,500–7,500		70–85	30–45	*Hearths*: N9/6-2. *Pits*: N11/12, N12/8-3
II	2a	7,500–18,000	Zone of large flake implements	85–105	45–65	*Hearths*: N5/15-13, M10/21. *Pits*: N5/25
II	2b	18,000–32,000		105–116	65–76	
II	2c	32,000	Discrete band of lithics and occupation debris	116–120	76–80	
II	2d	>32,000		120–145	80–105	

* These are indicative depths for the Main Trench. The thickness and the elevation of the layers and horizons vary across the rock shelter.

that can be used to integrate material from different trenches. They also provide an independent crosscheck of my interpretations of lithostratigraphy and chronology (^{14}C and TL). Figure 4 shows that all three lines of evidence (lithostratigraphy, cultural stratigraphy and chronostratigraphy) essentially knit the site together in the same way.

These analytical units allow a spatial component to be incorporated into various analyses. With such an approach, there is always a risk that fine-grained temporal trends will be obscured, creating a false impression of sharp strophic change—as Frankel (1988) cautions. An alternative approach is to analyse a stratigraphic column from a single grid square. The main limitations of the latter are smaller sample sizes and the difficulty of integrating results from different grid squares or trenches. (Note: as layers vary in thickness and absolute height across the site, generalized age-depth data are a poor guide to grouping spits for analysis). In this study, I have routinely crosschecked one type of analysis against the other

Table 2. Grouping of excavation units by analytical unit.

grid square	analytical unit 1a	1b	1c	2a	2b	2c	2d
M9	1–2	—	—	—	—	—	—
M10	1–4	5–10	11–14	15–22	23–25	26	27–28
M11	1–4	5–9	10–14	15–23	24–26	27–28	29–33
N5	1–4	5–8	9–14	15–25[h]	—[j]	—[j]	27
N6	1–3	4–8	9–17	18–20	—	—	—
N9	1–3	4–5	6	7–9	10–11	—[k]	12
N10	1–3	4–5	6[g]	8–10	11	—[k]	12–13
N11	1–4	5–10	11–16	17–26	27–29	30–31	32–35
N12	1–4	5–6	7–8	9–20	21–25	25–27[l]	28–35
N13	1–4	5–10	11–13	14–19	20–22	23–24[m]	25–28
N18	1–2	—[f]	—[f,g]	8–12	13–17	18	19–22
QR9	1–2	3–4	5[g]	7–9	—	—	—
ST5	1–2[e]	—[f]	—[f]	—[i]	—	—	—
Z9	1–6	—[f]	—[f]	26–38	39	—	—
Z10	1–2	—[f]	—[f]	6–8	9–10	—	—

[e] The top 10 cm of the profile is arbitrarily taken to represent 1a because overall artefact densities are too low to delineate the lower boundary of the unit.
[f] There is insufficient data here to distinguish between units 1b and 1c. N18/3-N18/6, ST5/3-ST5/7, Z9/7-Z9/25 and Z10/3-Z10.5 are therefore "unassigned layer I".
[g] Spits which straddle the interface of layers I and II (N10/7, N18/7, QR9/6) are "unassigned layer II".
[h] N5/25 is a pit containing material derived from the level of N5/19. Therefore units N5/19-25 are combined for most analyses.
[i] The concentration of coarse debitage and other large items against the wall of the shelter in ST5 make it difficult to isolate the changes in mean artefact size that characterize 2a. ST5/8-ST5/10 are therefore "unassigned layer II".
[j] N5/26 is "unassigned layer II" as it is from an area disturbed by the N5/25 pit.
[k] The 32,000 B.P. surface was not recognized during the initial excavations in 1986. The recording methods used in N9 and N10 do not allow artefacts to be securely assigned to unit 2c.
[l] Material from N12/25 is excluded except for individually levelled-in artefacts with depths of 116 cm below datum.
[m] Material in N13/25 is stratified immediately beneath the floor, and can be grouped with 2c for some analyses.

Table 3. Overall composition of the flaked stone assemblage. Data are numbers of artefacts (6 mm sieve fraction) in each category.

analytical unit	retouched artefacts	unmodified flakes flakes	cores	debitage	total number number
1a	319	996	34	5878	7227
1b	153	531	14	3096	3794
1c	59	317	11	1269	1656
unassigned layer I[e]	66	425	28	1809	2328
2a	81	430	39	1046	1596
2b	4	76	2	157	239
2c	2	11	—	29	42
2d[f]	—	9	1	12	22
unassigned layer II[g]	3	34	2	126	165
total number	687	2829	131	13422	17069

[e] 1b and 1c cannot be separated in some trenches (N18, ST5, Z9/Z10).
[f] One core and 5 flakes are doubtful artefacts and excluded from further analysis (see text).
[g] Mainly artefacts from the interface of layers I and II in N10, N18, ST5 and QR9 where the upper limit of 2a is poorly defined.

(see Figs 14 and 20), testing any differences between analytical units (with their larger sample size and spatial perspective) against trends in individual stratigraphic columns (with limited sample size but finer-grained temporal data).

Table 1 shows the relationship between layers, identifiable cultural horizons and analytical units. Table 2 summarizes the grouping of excavation units (spits) into analytical units. Each of the analytical units is described below.

Unit 1a: Late Holocene horizon (0–800 B.P.). The greatest concentrations of chipped stone artefacts, grindstones, ochre, charcoal, bone and eggshell occur in the upper 5–10 cm of the deposit across the site reflecting a substantial increase in the level of use of the rock shelter from about 800 B.P. As well as a dense horizon of occupation debris, this phase of use left a series of hearths, pits and ash lenses across the site.

Unit 1b: (800–3,500 B.P.). With one exception, geometric microliths and tula adze slugs are restricted to units 1a and 1b in the upper 25–30 cm of the deposit. Their stratigraphic distribution is used to divide the deposit beneath unit 1a into a horizon containing microliths and adzes (unit 1b) and an underlying horizon, pre-dating the major use of small-tool phase artefacts at this site (unit 1c). In trenches where there are too few geometric microliths and tula adze slugs to make this assessment (N18, ST5, Z9/Z10), the deposit beneath unit 1a is simply listed as "unassigned layer I" (Table 3). Law (2003:118–126) suggested the base of unit 1b may be as old as 6,000 B.P. but based his argument on selective use of the ^{14}C date series. In fact, the base of unit 1b is bracketed by ANU 6602 (2,640±70 B.P.—unit 1b) and Beta 18882 (5,860±150 B.P.—unit 1c).

Unit 1c: (3,500–7,500 B.P.). Material from the lower part of layer I is grouped together as unit 1c.

Unit 2a: large flake implement horizon (7,500–18,000 B.P.). Large flake implements >50 g and steep-edged scrapers occur in the upper part of layer II. During excavation, the greatest concentration of these implements appeared to be between 95–98 cm below datum, but subsequent tabulation of finds shows that this is just the central part of a broader horizon of large flake tools at depths between 85 cm and 105 cm below datum. In stratigraphic terms the horizon occupies a band 20 cm thick within the top of layer II. Its central part is well dated between 10,500 B.P. and 12,000–13,000 B.P. and the horizon must span the time period from about 7,500 B.P. to c. 18,000 B.P. (Note: an earlier study by Smith *et al.* (1998) used a preliminary age estimate of c. 13,000 B.P. for the base of 2a. The implications of this are discussed below in "History of the rock shelter"). Several features are associated with this horizon—the N5/25 pit and M10/21 hearth—and some, if not all, of the petroglyphs at the site.

Unit 2b: (c. 18,000–32,000 B.P.). Material beneath the large flake horizon, but stratigraphically above the 32,000 B.P. palaeosurface, is grouped as unit 2b. A division into units 2b and 2c is only possible in the Main Trench.

Unit 2c: pre-glacial surface (c. 32,000 B.P.). This is a thin band c. 2 cm thick of stone artefacts, charcoal and pellets of red ochre extending across N11–N13 and M10–M11 in the central part of rock shelter at depths below datum between 116–120 cm. Judging from the narrow vertical spread, this material was deposited on a palaeosurface of some kind, although this surface could not be defined during excavation or identified in sediment thin-sections. Attempts to refit artefacts from this level were unsuccessful although several artefacts clearly relate to the same knapping event. It is possible that unit 2c represents a palimpsest of material from several visits, perhaps accumulated on the surface over some time, rather than an assemblage of strictly contemporaneous material.

Unit 2d: (>32,000 B.P.). The excavation uncovered a small number of artefacts stratigraphically lower than the 32,000 B.P. palaeo-surface. These fall into two groups. The first includes red ochre, sandstone, silcrete and chert flakes, and debitage, all from spits immediately beneath the 2c palaeosurface in the Main Trench (16 artefacts in total). This material is unlikely to be much older than 35,000 B.P. The second group consists of five small flakes and a possible core, from the base of Layer II, from widely separated find spots across the site. A small piece of red ochre was also recovered from this level. Whether these lithics are human artefacts or naturally flaked pieces, or artefacts possibly displaced from a higher level, is unclear and they are therefore excluded from the analysis (but see "History of the rock shelter" for description of these finds).

Where the cultural stratigraphy is not well resolved, some analytical units cannot be isolated. In fact, 15% of artefacts are from spits that cannot be securely assigned to one or another of these units (Table 3: "unassigned layer I" or "unassigned layer II"). My aim is to provide optimal separation of diachronic assemblages, based on internal stratigraphic markers, rather than assign all spits to a unit. Therefore, I am critical of Law's analysis of retouched flakes, which arbitrarily re-allocates spits between units 1b and 1c (Law, 2003: 151), potentially obscuring differences between these units.

Materials and methods

Recovery and sorting. During excavation all material was sieved through nested 6 mm and 3 mm sieves and bagged according to excavation unit. Sorting of sieve residues and the separation out of flaked stone artefacts from these residues was carried out in the laboratory. The only exceptions to this routine were artefacts recorded during excavation ("levelled finds"), which were given individual find numbers and bagged separately. The 6 mm fraction was sorted in its entirety and some 17,069 artefacts were recovered (Table 3). However, it was difficult and time consuming to separate the fine chipping debris (flakelets) from the 3 mm sieve fraction. After wet sieving, and the removal of charcoal by flotation and manual sorting, the bulk of this fraction was made up of finely comminuted sandstone gravel, containing up to 300 flakelets per kg. Therefore, separation of fine flaking debris from the 3 mm sieve fraction was undertaken for only selected stratigraphic columns (N5, N10 and M10).

Artefacts from the 6 mm fraction were sorted into several broad classes as follows:

Retouched artefacts. Pieces or flakes with secondary flaking. Fine edge damage (chattering or nibbling) was ignored but artefacts with more marked edge damage or utilization were included. Many of the artefacts are pieces of large implements or small fragments of a retouched edge.

Unmodified flakes (≥1 cm^2). Both complete and broken flakes. In the case of broken flakes, only proximal ends, where the striking platform or bulb of percussion could be identified were included. This follows Andrefsky (1998: 88) rather than the more precise calculation of MNF (minimum number of flakes) given in Hiscock (2002: 254), which incorporates counts of distal fragments. At Puritjarra, I was not confident that MNF could be accurately determined given that distal flake fragments on local silicified sandstone were difficult to distinguish from shatter fragments or natural spalls of this material.

An arbitrary lower size limit of 1 cm^2 was used to exclude very small artefacts from this class. Flakes less than 1 cm^2 are unlikely to be systematically recovered in a 6 mm sieve mesh. I have followed procedures advocated by Johnson (1979: 69, 97, 157) who argued that size data should be

filtered using a slightly higher size threshold to clean up the data and ensure comparability between excavation units.

Cores. These are pieces serving as a primary source of flakes. Any piece from which at least three flakes (≥10 mm long) have been struck was classified as a core unless there were other grounds for including it as an implement.

Debitage. All remaining artefacts—including shatter fragments, chips, flakes <1 cm^2, distal or medial fragments of flakes, and amorphous flaking debris—were classed as debitage. A distinction was made between debitage from the 6 mm sieve fraction and the fine chippage recovered from the 3 mm sieve. The latter is not included in any counts unless explicitly stated.

Cores and retouched artefacts were further classified according to category or type. Details are given below. Existing typological schemes were used so that the Puritjarra artefacts could be compared with other assemblages, even though it is now clear that some of the forms described are reduction states rather than formal types (cf. Hiscock & Attenbrow, 2003). These typologies also represent a useful starting point for developing a first-order characterization of an assemblage, as they include a range of artefact morphologies which are widely understood and readily re-interpreted from a range of perspectives (either as reduction states of particular implements, debitage from specialized knapping processes, manufacturing blanks, formal or functional implement types).

Sampling the assemblage

Flake attributes. Trends in flake weight over time, or by raw material, or zone within the shelter, were examined using the entire assemblage of flakes (N=2829).

For detailed *attribute* analysis (for attribute definitions see Appendix 1), a sample of 931 flakes was drawn with several factors in mind. First, only flakes for which platform variables could be measured were recorded. Second, in practical terms it was more efficient to use excavation units as the basis for sampling rather than attempt to locate individual flakes within the collection. Once an excavation unit was chosen, all unretouched flakes ≥1 cm^2 were described. Third, the sample had to be drawn in a way that took intra-site spatial variability into account. These constraints were met as follows.

- All flakes from layer II were recorded, giving as large a sample of flakes from 2a–d as possible.
- In layer I, all flakes from N11 and N5 were recorded giving a continuous stratigraphic column at two points within the shelter. The numbers of flakes in N11 and N5 also provided an adequate sample of material from units 1b and 1c.
- To strengthen data on spatial variability within the shelter, I also recorded all flakes from the uppermost excavation units in N5 through to N18, giving a transect from the rear of the shelter to the lip of the overhang.
- Flakes from QR9 were added to this sample to provide a sample of the larger artefacts tending to accumulate in and around the rock fall in the centre of the shelter.

Raw materials. In the tables below, I have not routinely broken down each analysis by raw material for two reasons. First, my analysis showed this duplicated trends shown by the wider assemblage. At Puritjarra, flaking methods are not strongly differentiated by raw material. It is blank form that is important and this cuts across raw material categories, as Barton (2003: 35) also found in Simpson Desert assemblages. Secondly, the sample is too small to calculate valid statistics for each raw material separately. Even with the larger sample provided by the wider assemblage, the data are often strongly skewed statistically.

Supporting data sets. Not all analyses can be reported in detail in this paper. Results can be checked using the databases listed in Appendix 2 (available on request from the author).

Multivariate analyses were carried out using MV-ARCH (Wright, 1992).

The Lithic Landscape

People visiting Puritjarra made extensive use of local materials for stone artefacts—silicified sandstone, clear quartz and ironstone—but throughout the history of the site they also brought in better quality stone from sources up to 60 km away—white chalcedony, nodular chert, and silcrete (Table 4).

Local materials

The sedimentary rocks forming the rock shelter provided a range of materials:

Silicified sandstone. The dominant raw material in all units is a low-grade orthoquartzite, found locally in beds c. 0.5 m thick within the Mereenie sandstone that forms the rock shelter (and exposed in places within the shelter itself). This material has a good conchoidal fracture. When fresh it is hard and brittle but older implements excavated from layer II during the damp conditions experienced in May 1988 were deeply weathered and had to be left to harden on drying. The immediate source of the silicified sandstone used by inhabitants of the rock shelter appears to have been roof fall, or blocks of stone from the scree slope on the southern side of the rock shelter. Flakes were also removed from the exposed edges of large rock slabs embedded in the floor of the rock shelter.

Black/brown ironstone. Thin beds of a fine-grained ferruginized rock occur near the junction of Mereenie sandstone and the underlying Carmichael sandstone. Locally referred to as ironstone, this material occurs as gravel within the shelter deposits and outcrops at the foot of the escarpment 1 km north of the rock shelter. It mainly occurs in tabular pieces c. 20 mm thick, which limits its utility.

Quartz. Small quartz pebbles c. 30 mm diameter occur in the local sandstone. These were occasionally used as sources of flakes.

Non-local materials

The transported stone provides a broad picture of the catchment used by the inhabitants of the rock shelter (Table

Table 4. Temporal distribution of raw materials at Puritjarra.

analytical unit	n	silicified sandstone %	iron-stone %	quartz %	grey silcrete %	other silcrete %	white chalcedony %	yellow-grey chert %	nodular cherts %	red siltstone %	glass[e] %
1a	7227	50	3	<0.5	6	1	27	6	6	<0.5	<0.5
1b	3794	47	4	<0.5	7	1	29	8	4	—	<0.5
1c	1656	67	4	1	5	1	17	3	1	—	—
2a	1596	49	5	<0.5	30	3	10	2	1	—	—
2b	239	54	6	—	30	5	4	1	—	—	—
2c	42	29	5	—	21	21	19	5	—	—	—
2d	22	64	5	—	27	—	5	—	—	—	—
total assemblage[f]	17069	53	4	<0.5	9	1	23	6	4	<0.5	<0.5

[e] A piece of clear glass (M10/1-7) was found in 1a just below the modern floor of the rock shelter. A retouched piece of green bottle glass (N13/6-1) was also recovered from unit 1b, where it is intrusive and associated with traces of a burnt tree root nearby (Feature N13/8).
[f] Figures for total assemblage include unassigned I and II.

5), although specific stone sources can rarely be identified. The inhabitants of Puritjarra used stone drawn from sources across a wide area west of the main ranges. One of the strongest connections was between Puritjarra and the Putarti Spring/Puli Tjulkurr area, where white chalcedony was obtained, at the end of the main ranges north east of the site (Fig. 1). This was an important link throughout the history of the rock shelter, mirroring a travelling route that Pintupi/Luritja people used in the ethnographic period (Puritjarra-Murantji-Alalya-Mt Udor-Putarti). The grey silcrete and tabular yellow-grey chert probably reflect use of local stone sources in the Cleland Hills or nearby in Watsons Range and the Glen Edith Hills. Other silcretes may have come from the main ranges 70 km east of Puritjarra. The use of nodular cherts suggest visits to the sand hill country south towards Lake Amadeus. Use of the sandhill country west of the Cleland Hills is unlikely to be reflected in the flaked stone at Puritjarra because this area is poor in isotropic stone. More surprising is the rarity of metasediments, vein quartz or igneous rocks from the Arunta complex which outcrop in a broad arc c. 50 km north of the rock shelter (Ranford, 1969).

Grey silcrete. A fine-grained grey silcrete forms a duricrust on sandstone or quartzite ridges throughout the central Australian ranges—especially on Mereenie sandstone and Heavitree quartzite. This is the most common material used for stone artefacts in the main ranges to the east of the Cleland Hills (Smith, 1988) and has often been quarried to produce the large leilira blades used as men's knifes (Graham & Thorley, 1996). In some archaeological studies it is confused with quartzite (Gould & Saggers, 1985; Saggers, 1982) but can be distinguished by its superior flaking properties, its lustre, and by the characteristic groundmass of clear amorphous silica that surrounds the quartz grains. Although useful exposures of this silcrete were not found near Puritjarra, it is likely that they exist elsewhere on the escarpments and sandstone surfaces that form the Cleland Hills. Fine-grained grey silcrete is the dominant material in excavations at the Tjungkupu site, in the Glen Edith Hills 35 km east of Puritjarra, so it must also outcrop in that area (Smith, 1988: chapter 5). Whatever the case, the silcrete entered Puritjarra rock shelter as flakes, small cores or retouched implements suggesting that much of the primary flaking took place elsewhere.

Table 5. Provenance of stone used for flaked stone artefacts at Puritjarra.

analytical unit	local stone[e] %	non-local stone sources in Cleland Hills %	non-local stone other regional sources[f] %	n
1a	53	12	34	7226
1b	51	15	34	3793
1c	72	8	19	1656
2a	54	32	14	1596
2b	60	31	9	239
2c	34	26	40	42
2d	69	27	5	22
LGM[g]	76	17	7	122

[e] Available in the rock shelter or nearby.
[f] 50–100 km from Puritjarra.
[g] Included in 2a and 2b but isolated here to show the distinctive pattern of stone usage in levels coinciding with the last glacial maximum.

Other silcretes. These are mainly red, brown or yellow fine-grained silcretes, available as fist-sized nodules or cobbles. This material occurs as a duricrust on sedimentary rocks in the main ranges east of Puritjarra. These silcretes are only a significant component of assemblages in early Holocene and late Pleistocene levels (units 2a–c), where they were brought in as unmodified flakes.

White chalcedony. The most abundant of the transported raw materials is white chalcedony. This is opaline silica, a cryptocrystalline material with strong conchoidal fracture, sometimes called "country opal". It varies from an opaque white chert to a translucent brown or grey chalcedony and occurs throughout the desert lowlands, usually in localized low outcrops. It does not outcrop in the Cleland Hills but several quarries are known to the north and west of this area (Hayden, 1979: fig. 29). The nearest source is a small quarry called Puli Tjulkura, literally "white stone", on the eastern side of Mt Peculiar 60 km to the north east of Puritjarra (Fig. 1). This quarry has not been used since the mid 1930s. Benny Pinapuka Tjapangati, a Pintupi/Kukatja man in his late sixties, specifically identified it as the main source of stone for people living in the Cleland Hills (Law, 2003: 71). He remembered visiting Puli Tjulkura as a boy with his family and walking back to Alalya, Murantji and Puritjarra with the stone, which men carried "tied up in their hair", pushed into the hair buns that young initiated men wore. PIXE-PIGME geochemical analysis confirms Puli Tjulkura as the probable source of the white chalcedony reaching Puritjarra from at least unit 2a onwards (Law, 2003: 66–67, Appendix A). The archaeological evidence shows that people brought pieces of chalcedony, mainly large flakes and shatter blocks <100 g, to Puritjarra rock shelter.

Yellow-grey chert. This is a cherty pedogenic silcrete, with occasional quartz grains set in a mottled yellow-grey chert groundmass. As it formed by induration of an ancient land surface it is widely found in the desert lowlands. This stone reached the rock shelter as large flakes and tabular blocks up to c. 300g. The nearest source has not been identified but there may well be an outcrop in the Cleland Hills, or in the surrounding dune fields.

Nodular cherts. The source of these bright yellow, black, buff, or semi-translucent yellow cherts probably lies in exposures of dolomite and limestone in the sandhill country south or south east of the Cleland Hills. One possibility is the Inindia formation between Watsons Range and Lake Amadeus, c. 60 km from Puritjarra. These cherts only become a significant component of the assemblage in the late Holocene (units 1a and b). The chert reached the rock shelter as small cobbles c. 25–50 mm diameter, often retaining the desert varnish that is characteristic of stones from stony "gibber" land surfaces. The chert cores are small 10–20 g and the size of the flakes and debitage is consistent with primary reduction of chert nodules rather than simply the trimming and resharpening of tools.

Red siltstone. Two flakes of a distinctive dark red siltstone are present amongst the excavated artefacts. There are a number of possible sources in the Cleland Hills and surrounding region, especially in the fine-grained sedimentary rocks of the Larapinta Group.

Metasediments and igneous rocks (not shown in Tables 4 and 5). These materials originate in the Arunta complex, north of the Cleland Hills. At Puritjarra, they are represented by two flakes of dolerite (Z10/3) and a section of a metasediment cobble (surface find)—all probably parts of ground-edged axes—and a trimming flake from a grindstone (ST5/2-3) also of metasediment. None of these finds are earlier than unit 1b.

Temporal changes in raw materials

Over time there is little change in the range of sources used except for the appearance of nodular chert after c. 3,500 B.P. (units 1a and b) (Table 4). However, there is an overall switch in the abundance of certain types of raw materials used for artefacts, from silcrete in the late Pleistocene and early Holocene, to chert and chalcedony in the late Holocene, when c. 40% of all artefacts were made of these materials. This is the product of a long-term trend—beginning around 7,500 B.P.—not simply a feature of the late Holocene (Fig. 5).

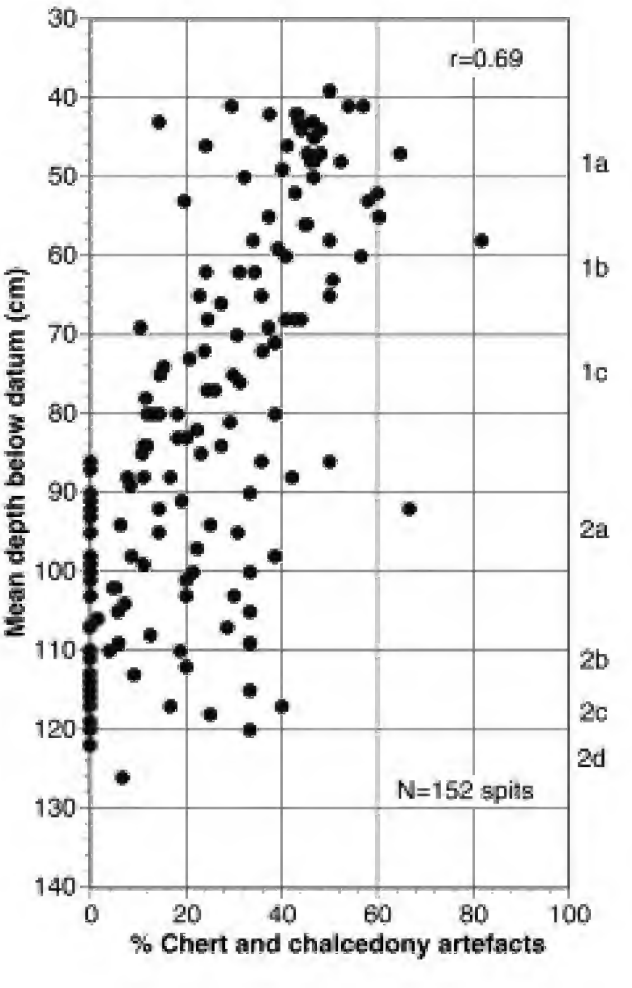

Fig. 5. Graph showing increasing use of chert and chalcedony over time. Data are number of chert and chalcedony artefacts per spit (excavation unit), expressed as percentage of total number of artefacts in each spit. The plot shows data for the Main Trench only (excluding the following: spits without lithics; spits in 2d with only doubtful artefacts, features intrusive from higher levels).

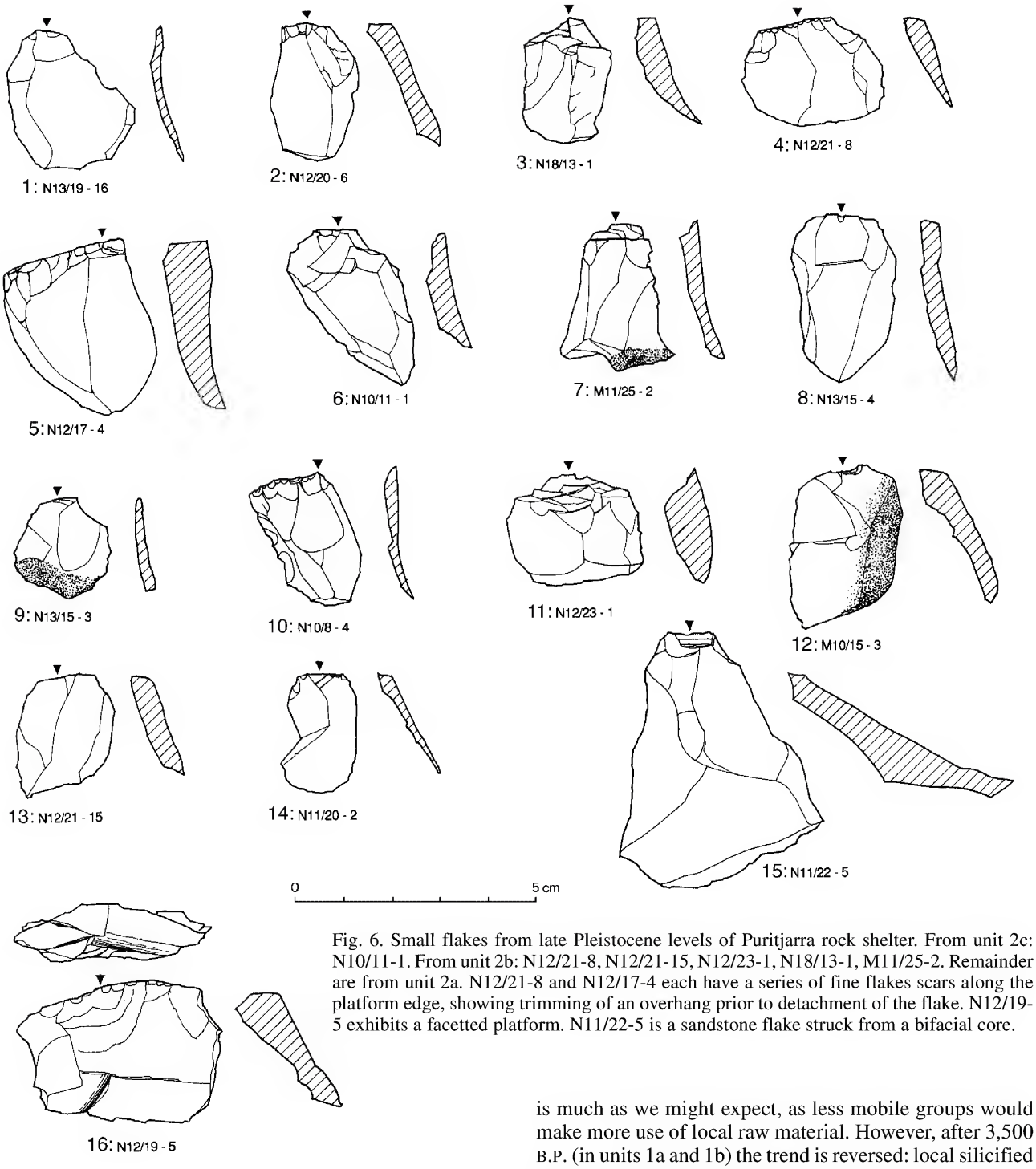

Fig. 6. Small flakes from late Pleistocene levels of Puritjarra rock shelter. From unit 2c: N10/11-1. From unit 2b: N12/21-8, N12/21-15, N12/23-1, N18/13-1, M11/25-2. Remainder are from unit 2a. N12/21-8 and N12/17-4 each have a series of fine flakes scars along the platform edge, showing trimming of an overhang prior to detachment of the flake. N12/19-5 exhibits a facetted platform. N11/22-5 is a sandstone flake struck from a bifacial core.

There are also changes in the relative importance of local versus transported stone (Table 5). People using the rock shelter at c. 32,000 B.P. (unit 2c) made comparatively little use of local sandstone and relied on silcrete and chalcedony from sources north and east of the Cleland Hills. There was greater focus on local stone during units 2a and 2b, particularly during levels coinciding with the last glacial maximum, but there is no evidence for a narrowing of the site catchment during the latter, as the use of materials from distant sources (chalcedony and exotic silcretes) continued.

The use of local stone increased during unit 1c (mid Holocene levels) as use of the rock shelter intensified. This is much as we might expect, as less mobile groups would make more use of local raw material. However, after 3,500 B.P. (in units 1a and 1b) the trend is reversed: local silicified sandstone appears to have been replaced by increasing use of white chalcedony despite a further increase in use of the rock shelter at this time. Possible reasons for this are discussed below (see "History of the rock shelter"). For instance, it may reflect (*a*) greater demand for cryptocrystalline materials imposed by a new tool-kit after 3,500 B.P. (see below); (*b*) changes in the accessibility of white chalcedony at the Puli Tjulkurra quarry; and (*c*) a switch in provisioning strategy from "embedded" procurement of stone (Holdaway & Stern, 2004: 80) to a logistical pattern as use of the rock shelter intensified in units 1a and 1b, or (*d*) greater residential mobility, resulting in more exotic stone being brought into the site.

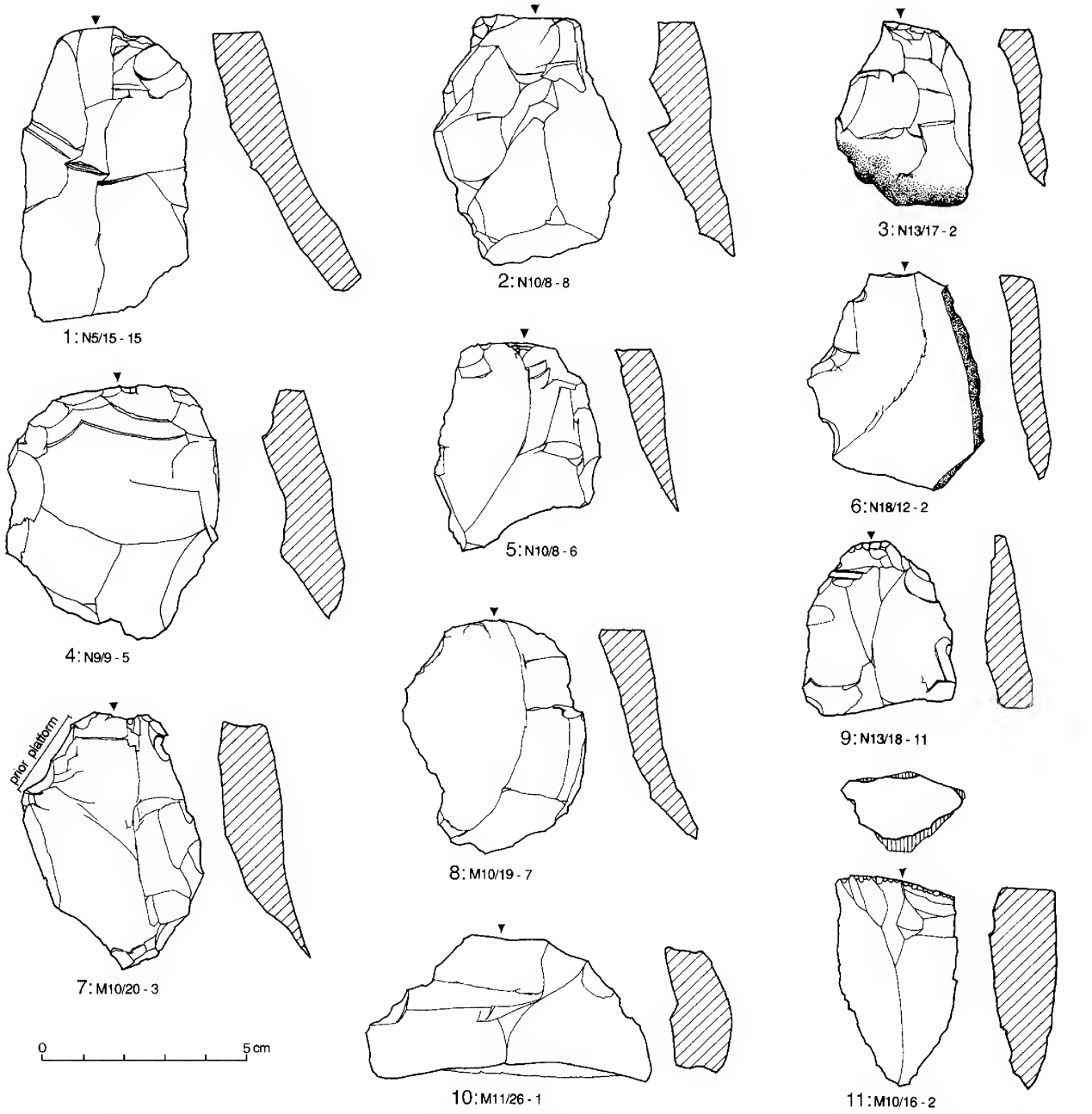

Fig. 7. Large flakes from late Pleistocene levels of Puritjarra rock shelter. All are from unit 2a except M11/26-1 (unit 2b). M10/16-2 is an ironstone flake struck from a horsehoof core, and has fine overhang-removal flaking along the platform edge. M10/20-3 is chert flake with evidence of a prior platform, showing that the core was rotated before this flake was detached.

Flake and core technology

Flakes. Flaking methods show little change over time. The inhabitants of the rock shelter generally produced small rectangular flakes with narrow platforms, often with crushing and step-flaking around the platform and with platform angles between 70° and 80° (Figs 6–8). There is an overall consistency in the *form* of the Puritjarra flakes throughout the history of the site (Table 6). This uniformity reflects generalized but not ad hoc flake production: there is little evidence for the uncontrolled shattering of blocks of stone described by Tindale at the Pulanj Pulanj quarry in the Tomkinson Ranges (1965: 139–143). Nor is there evidence for specialized flaking techniques or the manufacture of standardized blanks, such as blades, lancet flakes, or the large "potlid" flakes used for tula adzes. Bipolar flaking is absent: a bipolar core previously reported for N10/3 has been re-examined and is part of a broken retouched artefact rather than a core. A small number of flakes (<2%) have facetted platforms (e.g., N12/19-5, Fig. 6-16). Around 5–10% of flakes also bear small regular flake scars along the platform edge showing where the edge of a core has been trimmed prior to flake detachment (N12/21-8 and N10/8-4, Figs 6-4 and 6-10; M10/16-2, Fig. 7-11). Neither of these techniques shows a strong chronological trend.

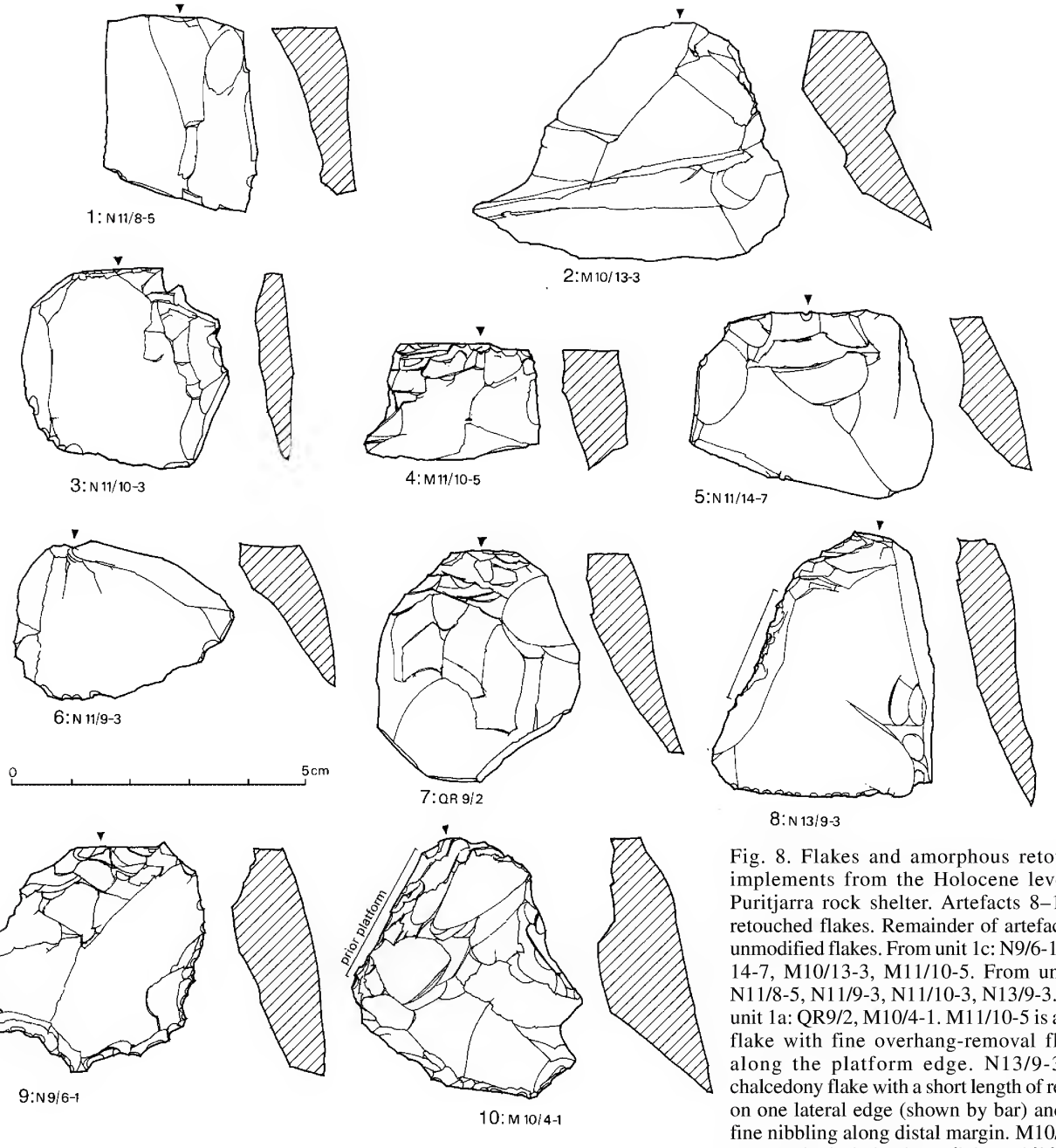

Fig. 8. Flakes and amorphous retouched implements from the Holocene levels of Puritjarra rock shelter. Artefacts 8–10 are retouched flakes. Remainder of artefacts are unmodified flakes. From unit 1c: N9/6-1, N11/14-7, M10/13-3, M11/10-5. From unit 1b: N11/8-5, N11/9-3, N11/10-3, N13/9-3. From unit 1a: QR9/2, M10/4-1. M11/10-5 is a chert flake with fine overhang-removal flaking along the platform edge. N13/9-3 is a chalcedony flake with a short length of retouch on one lateral edge (shown by bar) and with fine nibbling along distal margin. M10/4-1 is a retouched chalcedony flake exhibiting a prior platform.

Fine-grained silcrete, yellow-grey chert and white chalcedony show similar patterns of flaking, though there is greater variability and a wider size-range for flakes made on local silicified sandstone (Table 7). Student's-*t* tests indicate there is no significant difference in mean flake weight, comparing white chalcedony and grey silcrete (t = 0.0946, $t_{0.05(2),192}$ = 1.973) or grey silcrete and yellow-grey chert (t = 0.7477, $t_{0.05(2),152}$ = 1.976) (Table 7—all units combined).

In a previous report (Smith, 1989: 99), two flake facies amongst the late Pleistocene/early Holocene artefacts were distinguished: small flakes c. 30 mm long made on imported silcrete or chalcedony; and large flakes c. 80 mm long made on local sandstone and silcrete. Both facies involved flakes struck from well set up and maintained platform cores. Now that a larger sample of excavated material is available we can see that these facies are part of a continuum: no bimodality is evident in flake size, whether we use weight or flake length to estimate this. Although their relative importance varies both kinds of flakes are present throughout units 2a–d and into 1c.

Temporal trends. Flakes in late Pleistocene levels (units 2b–d) are small and well made with an emphasis on fine-grained silcrete—similar to late Pleistocene flakes at Kulpi Mara (Thorley, 1998b: 236). Over time there is a trend from 2a to 1a towards smaller flakes (Fig. 9). This is partly because flakes in unit 2a are more variable in size than those in other units and include many large flakes >40 mm long (mainly made on local sandstone or ironstone). These large flakes are less common in units 1c and 2b–d but still

Table 6. Flake attributes, (n = 764). Data are for all complete unmodified flakes included in the attribute study, except 5 flakes at the base of layer II (unit 2d), which may not be cultural artefacts. All figures are mean values except where indicated otherwise. As these data are strongly positively skewed, median weight is given for comparison.

analytical unit	n	median weight g	mean weight g	L mm	B mm	Th mm	platform thickness mm	exterior platform angle	L/B ratio	flare[e]
1a	229	1	3±6	21±10	18±8	5±4	5±3	72°	1.3	1.6
1b	74	2	4±7	23±10	20±9	6±4	6±5	71°	1.2	1.8
1c	84	3	8±13	27±14	24±12	7±5	7±5	68°	1.2	1.5
2a	286	4	12±19	30±15	27±13	7±5	7±5	75°	1.2	1.6
2b	69	2	4±6	23±9	20±10	5±3	5±4	71°	1.3	1.8
2c[f]	8(6)	2	24±36(3)	35±20(24)	26±13(19)	9±9(4)	7±9(3)	72°(74°)	1.4(1.4)	2.0(2.2)
2d	4	1	3±4	20±8	18±13	4±3	6±4	76°	1.4	1.4
unassigned II	10	1	2±2	19±6	18±4	3±2	4±2	74°	1.1	1.4

[e] This is Hiscock's parallel index (1986:48), calculated by dividing flake breadth by platform breadth. Values <1 indicate a flake that converges to a point. Values >1 indicate a flake with a distal flare.

[f] Values for unit 2c are skewed by 2 large sandstone flakes >85g. Figures in brackets exclude these.

represent a significant component of these assemblages. In contrast, the majority of flakes in units 1a and 1b fall between 10 and 30 mm in length. This size trend (expressed in terms of weight in Table 7) is also evident in the sandstone flakes and does not simply reflect greater use of chert and chalcedony in the late Holocene.

Flakes from units 1a–c also tend to have come from more heavily worked cores than those in earlier levels: there is more evidence of core rotation, more dorsal scars on the flakes, and more artefacts with flaked platforms. A multivariate (canonical variates) plot (Fig. 10) shows the centroids for 5 groups of flakes and plots these against flake variables: raw material grain-size, flake weight, percentage cortex, length, breadth, thickness, platform breadth, platform thickness, exterior platform angle, platform preparation, overhang removal, evidence of core rotation, and the number of flake scars on the dorsal surface. Vector 1 represents reduction stage. Flakes on the left-hand size of the plot tend to have come from heavily worked cores. Vector 2 represents flake size. Artefacts towards the top of the plot are larger flakes, with larger platforms, and tend to be on granular materials such as sandstone or silcrete. The overall trend over time is for smaller flakes, detached from more heavily worked cores, with more frequent use of fine-grained or cryptocrystalline materials. One anomaly in this pattern is that the frequency of cortex is not correlated with flake size. This is because most flakes in this assemblage are tertiary flakes and there are few decortication flakes at any level (Table 8).

Cores

There are only a limited range of cores present in the Puritjarra assemblage (Figs 11 and 12) and these show little change over time apart from a trend towards more intensive reduction of cores in the Holocene. The major types described below are consistent with the range of cores described for neighbouring parts of the arid zone (Barton, 2003; Cane, 1984, 1992; Gould, 1977; Smith, 1988).

Amorphous cores. These cores do not have discrete striking platforms and there is no detectable pattern in flaking. Essentially, they reflect opportunistic flaking of local sandstone. Flakes have been removed haphazardly from any convenient face, each flake from a different point on the core.

Bifacial cores. In this technique flakes have been detached from alternate faces along an edge. Heavily worked cores acquire a distinctive discoidal form with a sinuous edge (N5/22-1, Fig. 11.2), but many of the cores at Puritjarra were discarded before this state was reached. The method was mainly used for slabs of local sandstone and is an effective way of removing flakes along an edge with minimal preparation of the piece. As a result these cores are very variable in size (from 6 g to 4 kg) and size of the core bears little relation to the size of the flakes produced (20–40 mm long).

Table 7. Variation in flake weight by raw material and unit, (n=603). Data are for complete unmodified flakes included in the attribute study. Only the most common raw materials are shown.

analytical unit	silicified sandstone		grey silcrete		white chalcedony		yellow-grey chert		nodular chert	
	n	mean wt (g)	n	mean wt (g)	n	mean wt (g)	n	mean wt (g)	n	mean wt (g)
1a–b	156	5±8	32	1±1	51	1±1	26	2±3	23	1±1
1c	63	10±14	4	1±1	10	2±2	2	2±1	1	0.8
2a	174	14±19	52	5±12	14	4±7	6	12±25	—	—
2b–d	36	8±16	29	2±1	2	4±4	2	1±0.3	—	—
all units combined[a]	437	10±15	117	3±9	77	2±4	37	4±11	25	1±1

[a] n=693. These figures include flakes from "unassigned II".

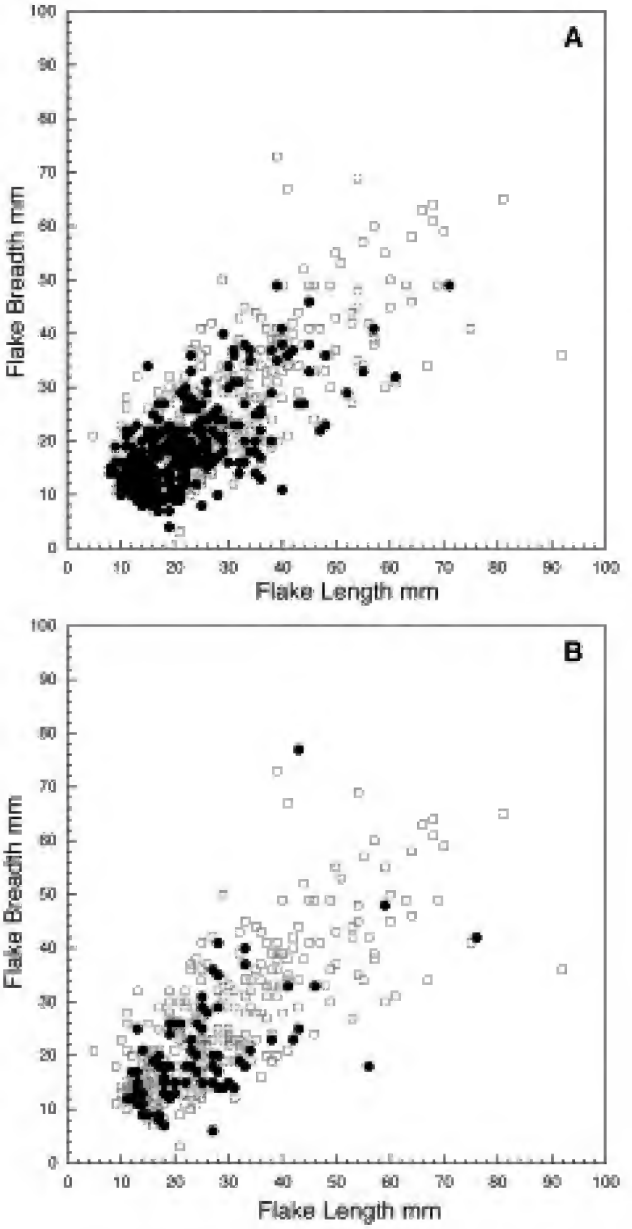

Fig. 9. Flake size and shape by analytical unit. Data are length/breadth measurements for a representative sample of 769 complete flakes. (*A*) Comparison of units 1a–b (solid grey circles), and unit 2a (open squares). Late Holocene flakes are smaller and less variable in size than early Holocene/terminal Pleistocene flakes, but have similar proportions. (*B*) Comparison of units 2b–d (solid grey circles) and unit 2a (open squares). Late Pleistocene flakes are smaller than those in the early Holocene/terminal Pleistocene, but have similar variability and proportions.

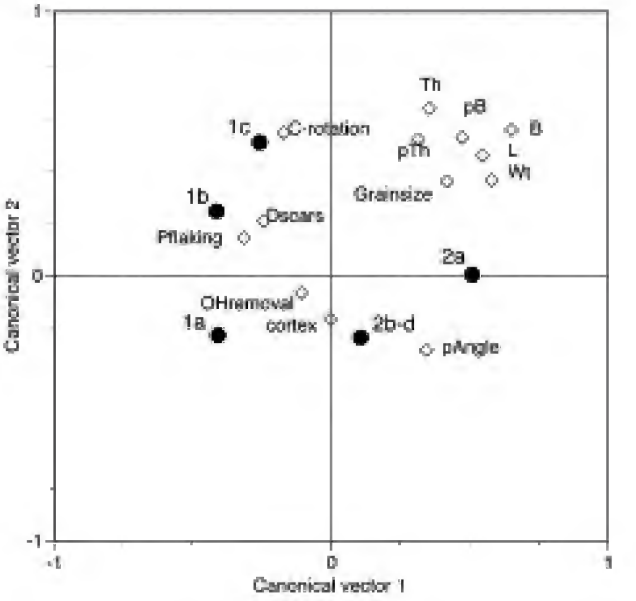

Fig. 10. Multivariate analysis of flake attributes, using the Canonical variates program in the MVARCH package. Data are for flakes where the full set of platform and flake attributes can be measured (N = 635). Scatter-plot shows the centroids for groups of flakes from each unit plots these against flake variables—raw material grain-size, flake weight, percentage cortex, length, breadth, thickness, platform breadth, platform thickness, platform angle, platform preparation, overhang removal, evidence of core rotation, and the number of flake scars on the dorsal surface.

Single platform cores. These cores result from the use of a bedding plane, or the ventral surface of a large flake, as a striking platform and the detachment of flakes down the face of the block. The majority of the cores at Puritjarra are single platform cores of one form or another. They range from cores on otherwise unmodified pieces of sandstone or silcrete (N13/19-1, N11/19-2, N9/9-3, N5/15-2) (Figs 11.1, 11.3, 11.5 and 11.8) to prepared cores showing evidence of attempts to prepare the core prior to flaking, by shaping the face of the core, modifying the platform or trimming the edge of the platform (N5/15-10, N9/9-2, ST5/4-4) (Figs 11.4, 11.7, 12.2). Chert or silcrete cores tend to be more heavily worked than those on sandstone, though many of the latter are also well developed (N13/19-1, N5/15-2, ST5/4-4) (Figs 11.1, 11.8, 12.2). From the early Holocene/terminal Pleistocene levels (unit 2a) there are several cores of grey silcrete (Z10/7-4, N9/9-2) (Figs 11.6, 11.7), of the type used to produce the small silcrete flakes shown in Fig. 6, for example, N9/9-2 (30 g). The platform on this core has been prepared by flaking, the overhang has been removed to facilitate knapping, and the removal of flakes extends around most of the perimeter of the core. From the flake scars we can see that this core produced flakes up to 22–25 mm long, with length/breadth ratios up to 2.8.

Multi-platform cores. Where a platform has given problems, a second platform has often been initiated on another face of the core. The majority of these multi-platform cores are ironstone or sandstone, reflecting the greater difficulty of flaking tough granular stone and the higher rate of platform failure on these materials.

Horsehoof cores. These are single or multi-platform cores with extensive step flaking undercutting the platform (N9/9-3, ST5/3-4, QR9/1-3) (Figs 11.5, 12.1, 12.4). The characteristic step flaking on these cores results when flakes repeatedly fail to run the length of the core. Unless a knapper can correct the flaw each step becomes a focus for further flake failure. At Puritjarra, "horsehoof" cores make up only a small component of the assemblage and are probably worked-out or "exhausted" cores. Although I have restricted the term to cores where the platform has been substantially

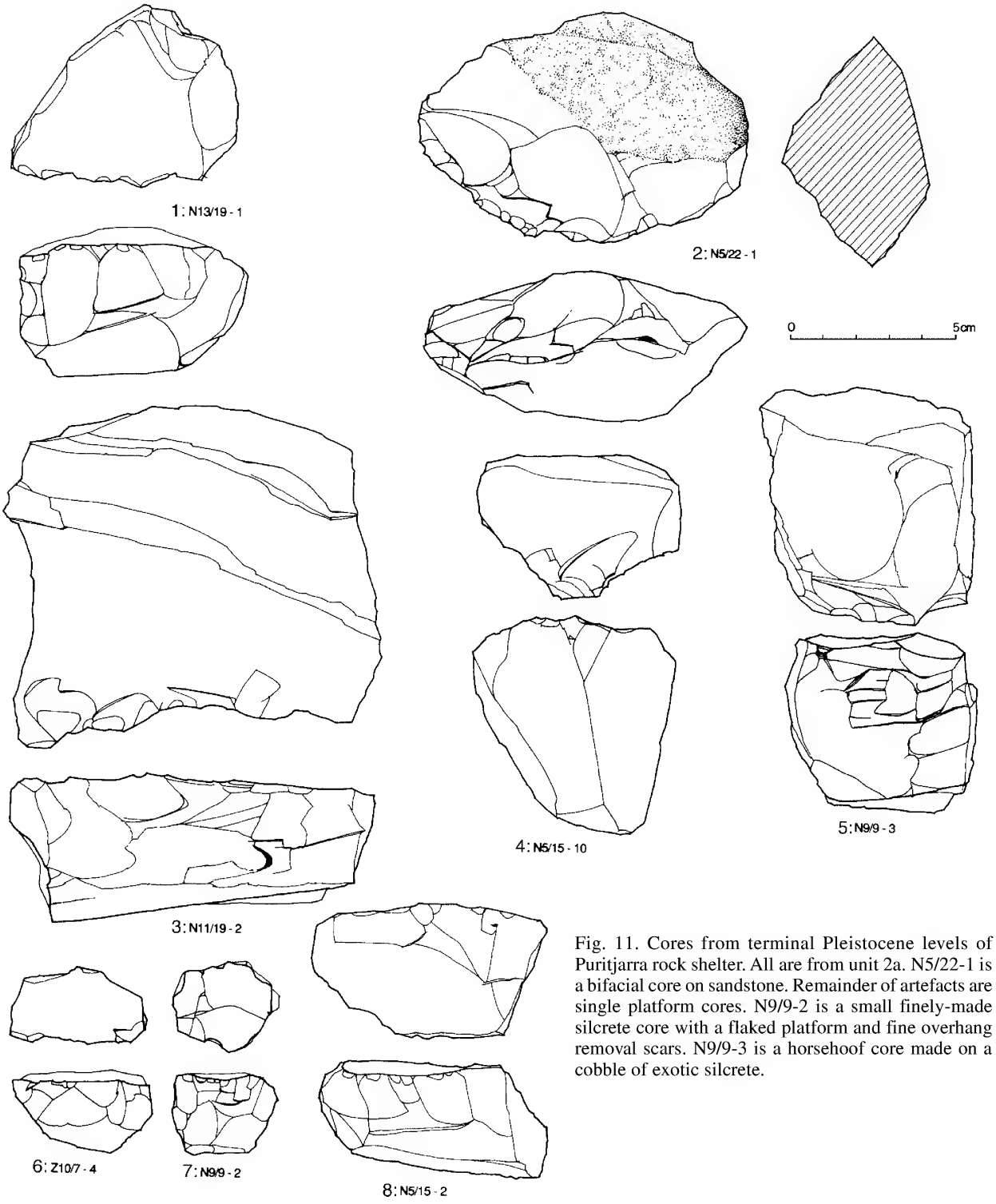

Fig. 11. Cores from terminal Pleistocene levels of Puritjarra rock shelter. All are from unit 2a. N5/22-1 is a bifacial core on sandstone. Remainder of artefacts are single platform cores. N9/9-2 is a small finely-made silcrete core with a flaked platform and fine overhang removal scars. N9/9-3 is a horsehoof core made on a cobble of exotic silcrete.

reduced by step-flaking, nested step-fractures are also evident on other platform cores (N13/19-1, ST5/4-4) (Figs 11.1, 12.2), showing that the "horsehoofs" are one end of a continuum in this assemblage.

The cores confirm the picture provided by the flakes. There is no evidence for specialized flake production, blades or bipolar techniques. The cores show a basic continuity in flaking methods and types of core preparation (Tables 9 and 10). The main chronological trend is towards heavier working of cores in the mid to late Holocene levels. Rotated or exhausted cores are more common in units 1a–c (Table 9). There is also a higher percentage of broken cores in these levels (e.g., N5/6-2, Fig. 12.8) (Table 10) and more cores with step-fractures around the platform (13% in 2a, 18% in 1c, 21% in 1b and 9% in 1a).

The use of cryptocrystalline cores increased in the late Holocene and there is a corresponding decline from unit 2a to units 1a–b in the mass of cores and in the size of the flakes detached from these cores (Table 10). This reflects more intensive reduction of cores in Holocene contexts not

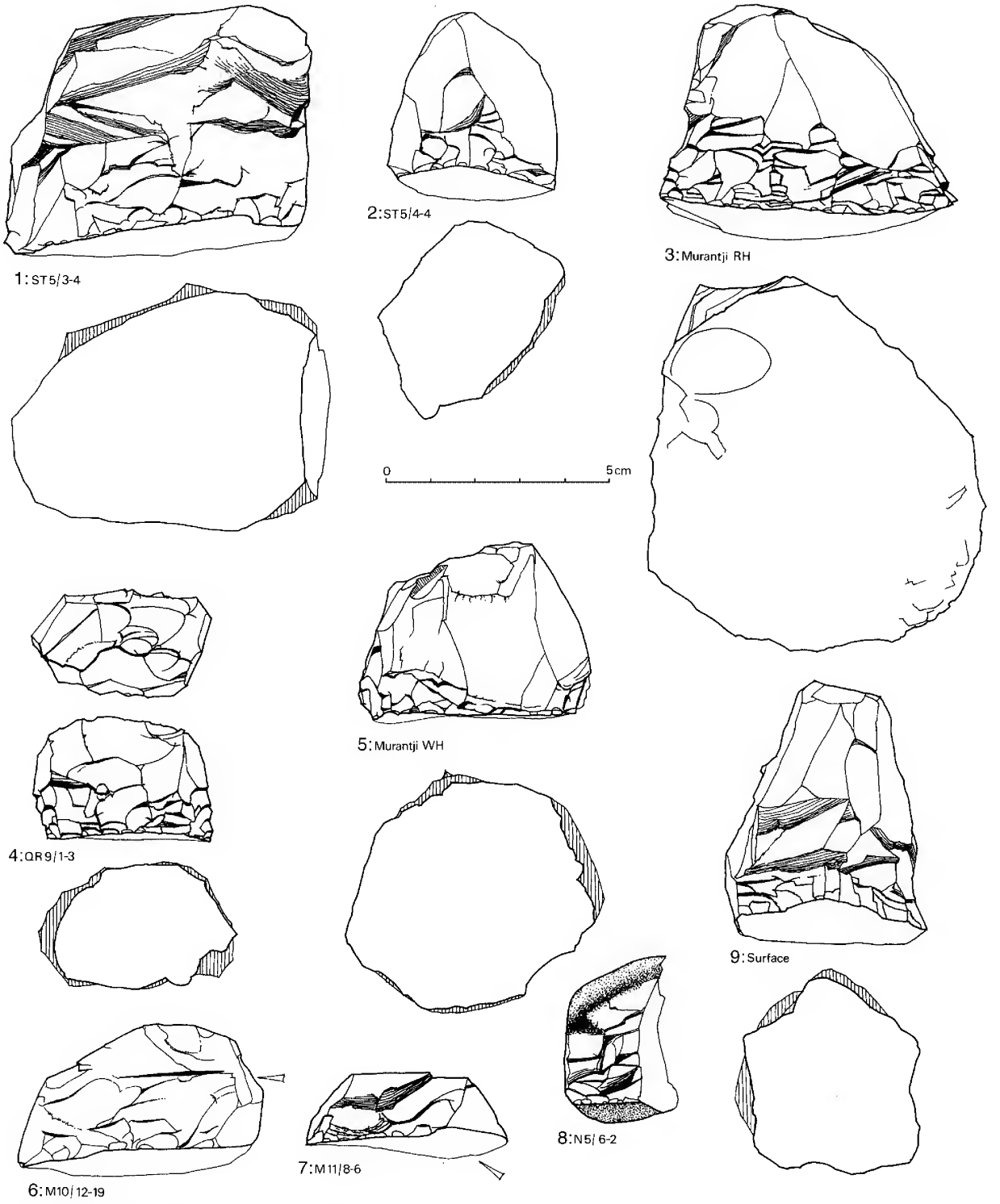

Fig. 12. Cores and redirecting flakes from the Holocene levels of Puritjarra rock shelter or from nearby Murantji rock hole. From unit 1a: QR9/1-3. From unit 1b: M11/8-6, N5/6-2. From unit 1c: M10/12-19. Unassigned 1b–c: ST5/3-4, ST5/4-4. M10/12-19 and M11/8-6 are sandstone redirecting flakes. N5/6-2 is a single platform core split during knapping. QR9/1-3 is a small horsehoof core, with a base (shown) reduced as a bifacial core. The large platform core from Murantji (3) is on a flake of yellow-grey chert.

simply a shift to finer-grained raw materials. For instance, although cores of silcrete and sandstone are larger on average than those made on chert and chalcedony (Table 11) they also became smaller after unit 2a. Multivariate analysis of the cores, using canonical variates, indicates an overall trend from unit 2a to 1a–c from large granular cores with cortex to smaller fine-grained cores discarded later in the reduction sequence with more frequent core rotation, larger platform angles and more frequent flaking of platforms.

Table 8. Flake stage, (n=515). Primary flakes have >50% cortex on dorsal surface. Secondary flakes are flakes with 1–50% cortex. Tertiary flakes have no cortex remaining on the dorsal surface.

	n	primary flakes %	secondary flakes %	tertiary flakes %
Unit 1a (late Holocene)				
All complete flakes	229	6	15	79
Grey silcrete flakes	24	4	21	75
Chalcedony flakes	38	8	26	66
Silicified sandstone	171	6	10	84
Unit 2a (Terminal Pleistocene)				
All complete flakes	286	7	13	80
Grey silcrete flakes	52	6	15	79
Chalcedony flakes	14	0	29	71
Silicified sandstone	189	8	13	79

Comparison of the cores and flakes identifies some missing elements of the assemblage. The Puritjarra assemblage, like most excavated artefacts, comprises the material that people discarded on-site rather than a representative sample of a stone industry. There is an overall correlation between the size of flakes and the size of cores in units 1a–1b but not for earlier levels. In units 2a–d there are few platform cores large enough to have been the source of the large flakes >50 mm found in these levels (except N5/15-10, Fig. 11.4). These flakes are on a range of materials. Silicified sandstone and ironstone predominate but there are also large flakes of grey silcrete, red/yellow silcrete, chalcedony and yellow-grey tabular chert. The large sandstone flakes probably derive from flaking of the boulders on the floor of the rock shelter. For other materials, it is possible that the cores remained in circulation and were carried away from the site. A chert core from nearby Murantji rockhole represents the sort of artefact missing from the excavated assemblage (Fig. 12.3). An alternative possibility is that large flakes were brought to the rock shelter rather than manufactured there. In units 2a–c the paucity of debitage from the working of chert, chalcedony or exotic silcrete suggests this is the more likely explanation.

In the late Holocene levels of the rock shelter, cores of nodular chert and yellow-grey chert are under represented (N=4) given the evidence for on-site flaking of this material. These small chert cores must have been curated and carried away from the site. In an ethnographic study in the northern part of the desert, Cane noted that his Gugadja informants had carried blocks of chert with them as they travelled but when people were more than a day's walk from an outcrop or quarry (about 15 km) access to fresh stone became more difficult. People then held onto their cores until worked out, explaining they had to "knock him, knock him" because there was "no djimeri this country" (Cane, 1984: 248). A similar process may have operated at Puritjarra in the recent past. In units 1a and Ib, there is no evidence to indicate chert cores have simply been worked to destruction: no bipolar reduction, no fragments of cores, broken cores are rare.

Redirecting flakes

Redirecting flakes result from the rotation of a core and subsequent removal of a flake running along the platform edge. Throughout the Puritjarra sequence most redirecting

Table 9. Number of cores by type and analytical unit.

analytical unit	n	amorphous cores	bifacial cores	single platform cores	multi-platform cores[e]	exhausted cores (horse-hoof morphology)[f]
1a	34	5	10	16	2	1[g]
1b	14	2	2	8	—	2
1c	11	1	1	5	3	1[h]
2a	39	5	7	23	3	1
2b	2	1	—	1	—	—
2c	—	—	—	—	—	—
2d	1	—	1[i]	—	—	—
unassigned layer I	28	5	2	16	3	2
unassigned layer II	2	1	—	1	—	—
total number	131	20	23	70	11	7

[e] These all have 2 platforms.
[f] Single platform cores unless indicated.
[g] One core (QR9/1-3) has also been worked as a bifacial core.
[h] Includes one core (N11/13-1)with 3 platforms.
[i] Doubtful artefact excluded from analysis.

Table 10. Core attributes. Data for complete cores are mean values unless otherwise indicated.

unit	complete cores					all cores				
	n	median weight g	mean weight g	core height mm	largest flake scar (L) mm	n	platform angle	granular stone[e] %	crypto-crystalline stone[f] %	broken cores %
1a	29	78	108±113	33±13	29±12	34	74°	74	26	15
1b	7	66	97±119	31±14	27±12	14	79°	50	50	50
1c	10	80	117±97	37±12	36±13	11	74°	82	18	9
2a	37	214	357±535	44±15	34±12	39	73°	95	5	5
2b	2	108	108±36	44±1	40±3	2	80°	100	0	0

[e] Silcrete and silicified sandstone.
[f] Chalcedony and chert.

flakes appear to have come from small or medium sized cores. Two large redirecting flakes removed from horsehoof cores are shown in Figs 12.6 (M10/12-19) and 12.7 (M11/8-6). There are proportionately more chert redirectors in units 1a and 1b than in earlier units (1a and 1b: 46%; 1c and 2a: 21%). In these levels the redirectors are also smaller and shorter reflecting the use of small chert cores.

Implements

The earliest tools (or fragments of tools) are from the palaeosurface dating to c. 32,000 B.P. (unit 2c) (Fig. 13). These include a chalcedony flake with a short length of shallow step-flaking or edge damage (M11/27-2), and a trimming flake of chalcedony (M11/27-4) struck off a tool that must have had a convex scraper edge with fine scalar retouch (Figs 13.2 and 13.4 respectively). From other levels prior to the last glacial maximum (unit 2b), there is a steep-edged scraper made on a thick sandstone flake (N10/11-4) and a thick step-flaked implement with a broad notch (N13/20-1, Fig. 16.6). Retouched artefacts are more common in terminal Pleistocene levels (2a) where they include steep-edged scrapers, notched implements, saws and a range of amorphous retouched or utilized artefacts. Irrespective of the type of implement, the tools in unit 2a are typically large thick flake implements >50 g, including steep-edged scrapers (QR9/8-2, N5/15-11, N11/22-2, QR9/8-11) (Figs 15.3, 15.4, 16.2, 16.3), saws (N10/9-1) (Fig. 16.9), and amorphous retouched implements (M10/22-2, N5/15-12) (Figs 15.2, 16.5). These types continue throughout the Puritjarra sequence but are joined by a suite of smaller finely worked hafted tools at c. 3,500 B.P. (Table 12, Group 2) and new types of grindstones for processing seeds (Smith, 2004). This new suite of tools is characteristic of late Holocene assemblages throughout central Australia (Smith, 1988) and is a regional variant of what is often termed the Australian small-tool phase (Mulvaney & Kamminga, 1999: chapter 14).

Cross-correlation of implement types. The spatial and temporal associations evident in a correlation matrix (Table 13)—generated by analysing the co-occurrence of implement types within the 336 excavation units (spits) at Puritjarra—suggest that there are two groups of implements at Puritjarra:

Group 1: Steep-edged scrapers, notched tools and saws.

Group 2: Geometric microliths, tula adze slugs, thumbnail scrapers and endscrapers.

This is a basic division between tools where only an edge has been modified and those that have been more intensively shaped. Amorphous retouched implements cut across this division and are associated with woodworking implements in both groups (tula adze slugs, thumbnail scrapers, steep-edged scrapers and notched implements). This is not especially surprising. The retouch on the amorphous retouched implements most likely represents use damage (utilization) or resharpening (Hayden, 1977) and this is more likely to have occurred on flakes used for woodworking than those used for cutting flesh or fibre.

Group 1 implements

Group 1 implements form a suite of hand-held woodworking tools. They were used throughout the Puritjarra sequence and show the same shift towards smaller artefacts and greater use of cryptocrystalline stone shown by the flakes and cores.

Table 11. Variation in core size by raw material and unit. Data are for complete cores.

analytical unit	silicified sandstone n	mean wt g	grey silcrete n	mean wt g	white chalcedony n	mean wt g	yellow-grey chert n	mean wt g	nodular chert n	mean wt g
1a–b	25	124±117	2	42±36	4	11±9	3	130±133	1	9.1
1c	7	125±106	—	—	—	—	1	33	—	—
2a	28	411±597	3	38±11	1	64	—	—	—	—
2b	2	108±36	—	—	—	—	—	—	—	—
total assemblage	84	241±383[e]	6	96±129	6	18±21	6	86±105	2	9±0.2

[e] This figure excludes M10/28-1, a bifacial core on a large sandstone block, weighing 4.1 kg, from 2d.

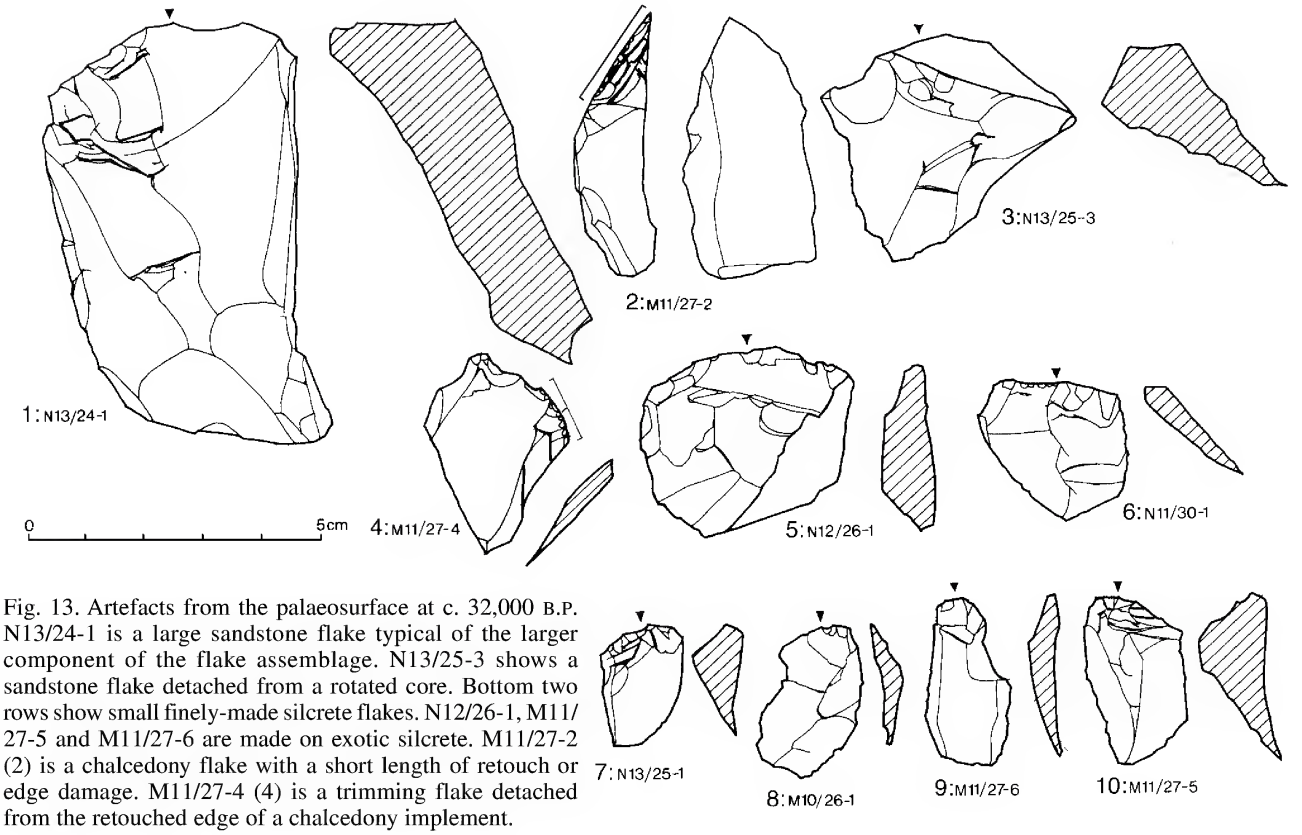

Fig. 13. Artefacts from the palaeosurface at c. 32,000 B.P. N13/24-1 is a large sandstone flake typical of the larger component of the flake assemblage. N13/25-3 shows a sandstone flake detached from a rotated core. Bottom two rows show small finely-made silcrete flakes. N12/26-1, M11/27-5 and M11/27-6 are made on exotic silcrete. M11/27-2 (2) is a chalcedony flake with a short length of retouch or edge damage. M11/27-4 (4) is a trimming flake detached from the retouched edge of a chalcedony implement.

Steep-edged scrapers. Implements with robust, steeply angled, step-flaked edges (cf. Holdaway & Stern, 2004: 230) are common throughout the Puritjarra sequence, but the form and presumably therefore the function of these tools changes over time. Ethnographic and experimental studies suggest implements of this type functioned as heavy duty woodworking tools (Hayden, 1977; Thomson, 1964; Tindale, 1941), and that the characteristic step-flaking results from edge damage or the resharpening of a steep edge rather than deliberate shaping of the tool. The implements from units 2a and 2b are thick artefacts with straight or concave edges, edge angles of >80°, and with step-flaking and crushing along the working edge. Many are made on large thick flakes of local sandstone, but there are also examples on yellow-grey chert (N11/19-1, Fig. 16.1), crystal quartz and chalcedony. In units 1a and 1b the steep-edged scrapers (Fig. 17) tend to be smaller implements (<20 g) made on medium-sized flakes, pebbles or small tabular blocks, usually of chert or chalcedony (64% in units 1a and b). Some are so small (57% <10 g in 1a) that they must have been hafted to have sustained the heavy step-flaking that is evident on their working edges. Unlike the implements from unit 2a, few late Holocene scrapers have concave working edges (23%); the majority have straight or convex edges. Table 14 suggests a trend over time to smaller implements with a concomitant reduction in the length of retouched edges. The pattern of use of these implements also changed over time. Most scrapers in unit 2a have >1 retouched edge. The Holocene implements tend to have only a single working edge, and there was a higher rate of breakage of these tools (Table 14). Overall, these changes probably reflect a change from hand-held woodworking implements towards the small, hafted scrapers or chisels used in the ethnographic period for trimming spear shafts and other wooden implements.

Notched artefacts. These are artefacts with one or more prominent notches formed by retouch, stepping or crushing on an edge (cf. Holdaway & Stern, 2004: 236–238). They are assumed to have functioned as spokeshaves on narrow spear shafts (Holdaway & Stern, 2004: 237–238; Mulvaney & Kamminga, 1999: 217). This is consistent with notch widths <20 mm. These implements were made on a variety of raw materials without regard for the form of the blank. Implements in units 1a and 1b are smaller than the notched implements in 2a but this is essentially a difference in the size of the blanks rather than notch dimensions (Table 14). The implements in 2a have slightly wider and deeper notches but the differences are too slight to be archaeologically significant. Like steep-edged scrapers, the pattern of use of notched implements seems to have changed over time. However, in this case, the late Holocene implements often have a second working edge and fewer are broken than those in terminal Pleistocene contexts (Table 14).

Saws. These are artefacts with finely dentated edges, made on flakes of local silicified sandstone, with regularly-spaced teeth c. 5 mm apart and 1–2 mm high on straight or convex edges (N10/9-1, N5/19-1, Figs 16.9 and 16.11) (cf. Holdaway & Stern, 2004: 238). Although saws are numerically not very important in the Puritjarra assemblage, they represent one of the few types of tools that can be said to have been carefully and deliberately trimmed to a predetermined form. The implements in units 1a and 1b

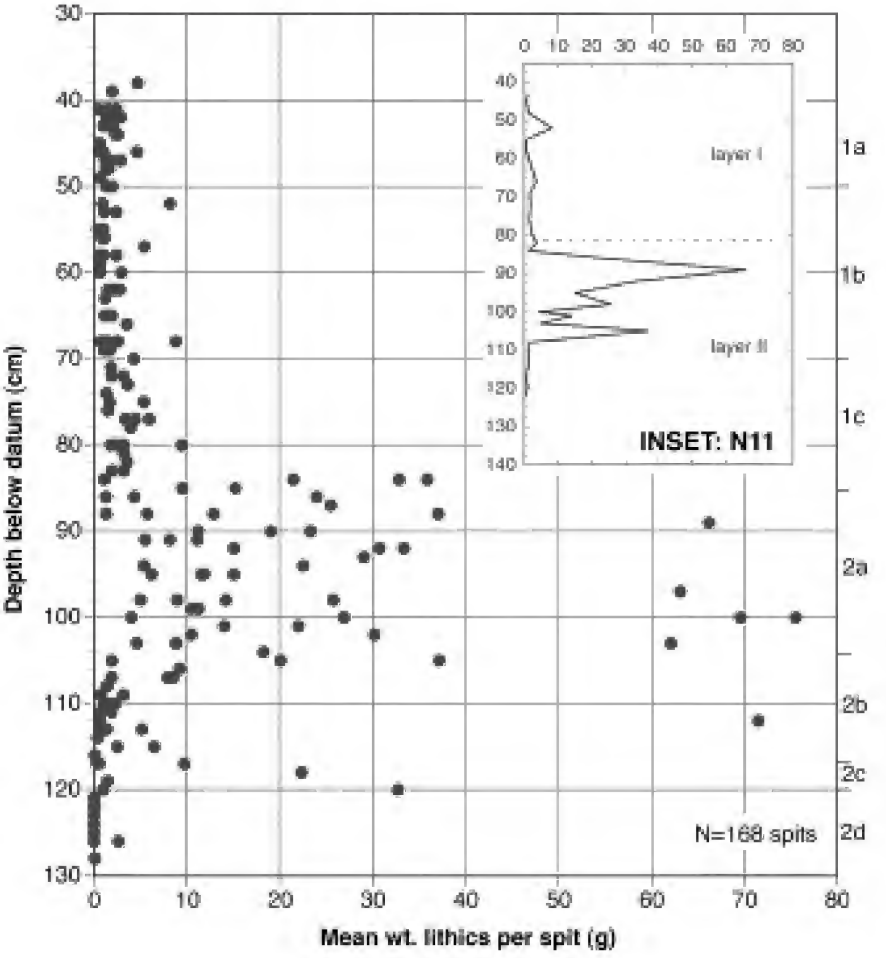

Fig. 14. Changes in the mean weight of artefacts over time, showing the concentration of large flake implements and large flakes in unit 2a (85–105 cm below datum). Plot shows data for the Main Trench, excluding doubtful artefacts from the lower part of 2d and intrusive pits or other features. Inset shows size trend in grid square N11. Data exclude N11/24-1, a large core (101 cm below datum) weighing 2119 g.

are smaller than those in 2a (mean wt.—1a and 1b:13±7 g, 2a: 60±29 g) but there is little difference in the length of working edge (mean retouch length mm—1a and 1b: 40±15 mm, 2a: 43±15 mm).

Other formal implements. QR9/8-1 (Fig. 15.1) has been carefully and deliberately worked and so warrants special mention. The blank is a large discoidal flake of silicified sandstone with a thick proximal end thinning out distally. This flake has been unifacially trimmed with shallow invasive flaking to a smooth convex edge with an edge angle c. 45°. The resulting edge is not sufficiently robust to sustain use as a scraper or chopper rather it seems best suited to working relatively soft materials with a slicing or cutting action. Microscopic examination of the edge for residues showed only soil starch to be present (see "Possible function of large implements" below).

Variability in Group 1 implements. Ethno-archaeological studies in the Australian desert have shown that—at least for edge-trimmed tools—a number of different morphologies could be used for the same function and that some of these forms simply represent episodes in the resharpening of an implement (Hayden, 1977—see also Hiscock, 1998 for a similar assessment). This is clearly a possibility with the Group 1 implements discussed here. Resharpening a thick serrated flake such as N10/9-1 (Fig. 16.9) could produce the steep concave working edges found on some steep-edged scrapers, such as N11/22-2 (Fig. 16.2), and further use could deepen this into a distinct notched edge resembling N13/20-1 (Fig. 16.6). However, at Puritjarra, the high variability within each class of implements makes formal statistical testing of these relationships difficult.

Group 2 implements

Group 2 artefacts (Fig. 18) represent a functionally heterogeneous suite of tools—spear armatures, adzes, and hafted scrapers—linked by a preference for chert and chalcedony and their function as elements of composite tools (as stone bits or barbs in multi-part implements made of wood, sinew and resin). Endscrapers are clearly an exception to this pattern as they are probably not components of composite tools: they may reflect specific ways of preparing tubers and fibrous roots rather than a new technology (O'Connell, 1974). At Puritjarra, Group 2 implements did not involve fundamental changes in flaking techniques: none of the new implements involved the production of blades or other specialized blanks (except perhaps tula adzes, which were not manufactured at the rock shelter). Rather, these technical developments appear to have centred around transformations of the wooden tool-kit associated with increased use of *Triodia* resin as a hafting cement.

Geometric microliths. These are small backed implements with abrupt blunting retouch along part or all of one side (cf. Holdaway & Stern, 2004: 262–264). Although not observed ethnographically, their use as barbs or armatures on spears is likely (see Kamminga, 1982; Mulvaney &

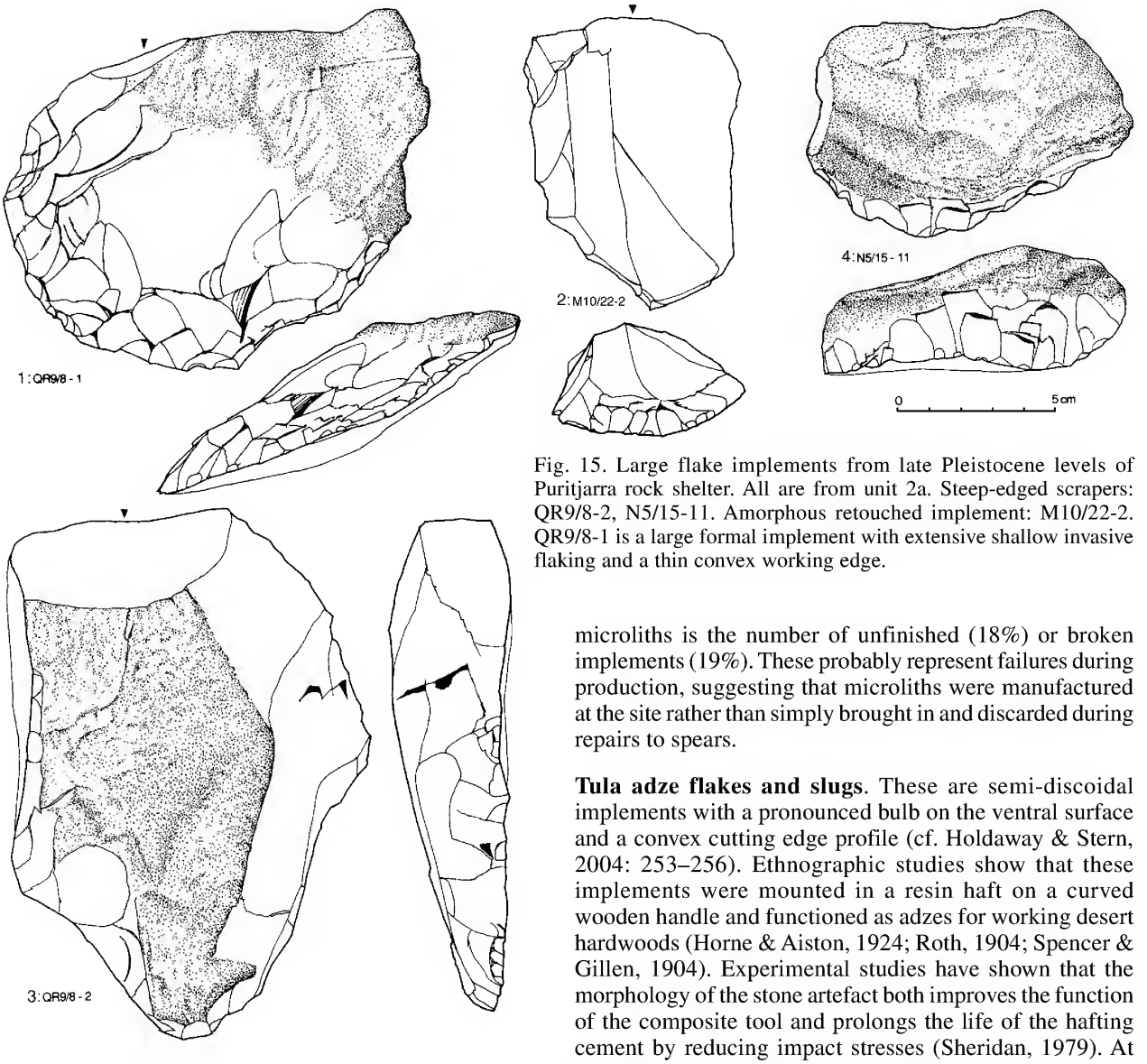

Fig. 15. Large flake implements from late Pleistocene levels of Puritjarra rock shelter. All are from unit 2a. Steep-edged scrapers: QR9/8-2, N5/15-11. Amorphous retouched implement: M10/22-2. QR9/8-1 is a large formal implement with extensive shallow invasive flaking and a thin convex working edge.

Kamminga, 1999: 235–236), although some may have served as small backed knifes, scrapers or incising tools. The geometric microliths at Puritjarra—like those elsewhere in Central Australia—are usually crescentic or triangular rather than trapezoidal in form and tend to be at the lower end of the size range for these implements (mean L 18±4 mm, B 10±2 mm, Th 4±1 mm, N = 38 complete specimens) (Fig. 18). Unlike sites in the Little Sandy Desert where backed asymmetric points are found (Veth, 1993: fig. 3.3), asymmetric forms are rare at Puritjarra and bondi points are not found. Microliths in unit 1a are slightly larger and squatter than those in 1b (mean L/B ratio, 1a: 1.8, 1b: 2.1) but the differences are probably not archaeologically significant. These implements are predominantly made on chert or chalcedony (79%) (N10/4-5, N9/3-4, Figs 18.2, 18.3) with the remainder on fine-grained grey silcrete (M10/6-1, M9/2-10, N6/5-2; Figs 18.1, 18.6, 18.8). The Puritjarra microliths are made on flakes rather than blades. This is generally the case in central Australia, though blades and blade cores occur in the late Holocene levels of some sites, such as Intirtekwerle, in the main ranges east of Puritjarra (Gould, 1978; Smith, 1988). One feature of the Puritjarra microliths is the number of unfinished (18%) or broken implements (19%). These probably represent failures during production, suggesting that microliths were manufactured at the site rather than simply brought in and discarded during repairs to spears.

Tula adze flakes and slugs. These are semi-discoidal implements with a pronounced bulb on the ventral surface and a convex cutting edge profile (cf. Holdaway & Stern, 2004: 253–256). Ethnographic studies show that these implements were mounted in a resin haft on a curved wooden handle and functioned as adzes for working desert hardwoods (Horne & Aiston, 1924; Roth, 1904; Spencer & Gillen, 1904). Experimental studies have shown that the morphology of the stone artefact both improves the function of the composite tool and prolongs the life of the hafting cement by reducing impact stresses (Sheridan, 1979). At Puritjarra, all the tulas are worn "slugs" (Fig. 18) except Z10/2-2 and M10/1-2 (not used because of a flaw in the edge of the tool). They are extremely variable in size, ranging from slugs on large flakes (M10/1-4) (breadth 47 mm) (Fig. 18.16) to very small slugs no larger than a thumbnail (N9/3-5) (breadth 17 mm). Most of the implements are on chert or chalcedony (88%) presumably because these materials hold an edge better than granular materials. Because heavy use and resharpening reduces the length of a tula relative to its breadth, the L/B ratio provides a rough measure of the condition of an implement. L/B ratios show that tulas in unit 1a (mean L/B 0.395) have marginally more wear than those in unit 1b (mean L/B 0.430). There is no evidence that adze flakes were manufactured at the rock shelter so the replacement of worn adzes must have involved blanks brought into the shelter from elsewhere.

Burren adzes. There are only five burren adzes in the excavated assemblage (e.g., Z9/9-2, Figs 18 and 19) (cf. Holdaway & Stern, 2004: 257). Their temporal distribution, raw materials and dimensions are similar to those recorded for tula slugs in the rock shelter. Therefore, they are probably best seen as a variant of tula use.

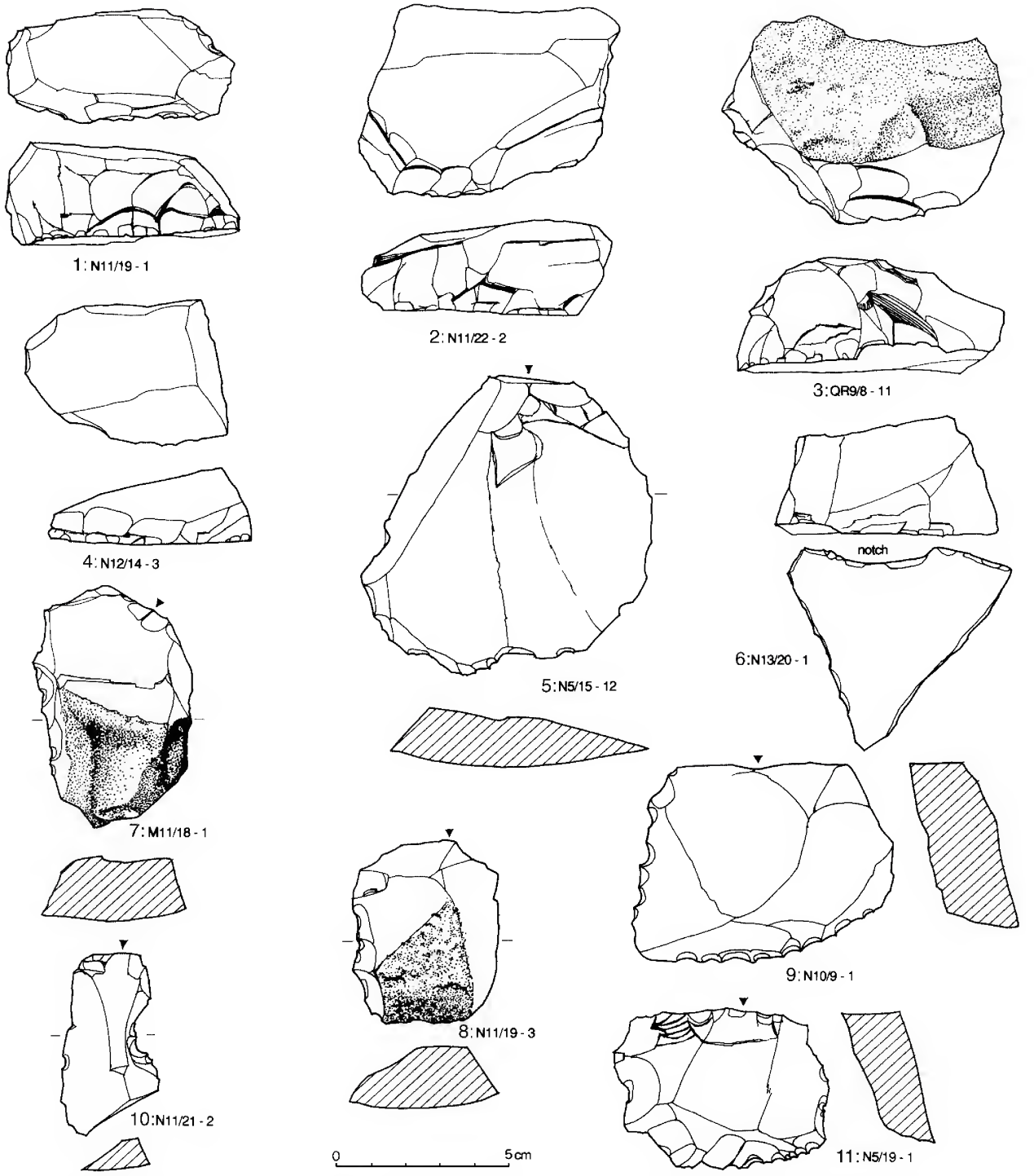

Fig. 16. Large flake implements from late Pleistocene levels of Puritjarra rock shelter. All are from unit 2a, except N13/20-1 (unit 2b). Steep-edged scrapers: N11/19-1, N11/22-2, QR9/8-11, N12/14-3. Amorphous retouched artefacts: N5/15-12, M11/18-1, N11/19-3. Notched implements: N13/20-1, N11/21-2. Saws: N10/9-1, N5/19-1.

Thumbnail scrapers. These are small discoidal scrapers, retouched to form a smooth convex edge on the distal margin (Figs 18.9 to 18.13) (cf. Holdaway & Stern, 2004: 234–235). They probably represent small, hafted scrapers. Like other Group 2 implements the thumbnails are mainly made on chert or chalcedony (73%) or on fine-grained silcrete. Some of the Puritjarra implements are large enough to have been serviceable as hand-held implements but many are too small to have functioned without some form of haft (mean L 15±3 mm, B 15±4 mm, Th 5±2 mm, N = 27 complete implements). Mulvaney & Kamminga (1999: 236) suggest that thumbnail scrapers were components of a spear armature ensemble. However, the pattern of wear on the Puritjarra implements is more consistent with woodworking or scraping fibrous materials: some thumbnails have steep step-flaked margins (M9/2-14) (Fig. 18.13), others have a polished rounded working edge with transverse striations (ST5/3-17, M9/2-13, N9/3-15). In Central Australia,

Table 12. Temporal distribution of flaked or ground tools and trimming flakes. Abbreviations: *I* and *II*—unassigned layers I and II.

artefact type	analytical unit									total number of artefacts per type
	1a	1b	1c	*I*	2a	2b	2c	2d	*II*	
Group 1										
Steep-edged scrapers	28	11	5	4	14	1	—	—	1	64
Notched implements	14	4	—	2	6	1	—	—	1	28
Saws	3	1	2	—	4	—	—	—	—	10
Other formal implements	—	—	—	—	1	—	—	—	—	1
Group 2										
Geometric microliths	29	17	1[e]	1	—	—	—	—	—	48
Tula adze flakes and slugs	23	10	—	1	—	—	—	—	—	34
Burren adzes	2	1	—	2	—	—	—	—	—	5
Thumbnail scrapers	23	6	—	1	—	—	—	—	—	30
Endscrapers	11	3	1[f]	2	—	—	—	—	—	17
Other retouched or utilized artefacts and trimming flakes										
Amorphous implements	121	60[h]	28	41	37	—	1	—	1	289
Fragments and trimming flakes	46	32	12	7	13	1	1	—	—	112
Redirecting flakes	19	7	10	5	4	1	—	—	—	46
Artefacts with use-polish	—[g]	—	—[g]	—[g]	2[g]	—	—	—	—	2
Grindstones[i]										
Seedgrinders	13	5	—	3	—	—	—	—	—	21
Amorphous grindstones	12	4	3	2	2	—	—	—	—	23
Grindstone fragments	24	2	5	12	2	—	—	1	—	46
Edge-ground tools										
Flakes from ground-edge axes	2	—	—	—	—	—	—	—	—	2
Hammerstones	—	—	—	—	2	—	—	—	—	2

[e] N6/15-1.
[f] M10/11-1, from the uppermost spit of 1c (see Figure 17-4).
[g] Indicates units where other retouched artefacts also have use-polish.
[h] Excludes N13/6-1, a glass artefact which is intrusive (see Table 4).
[i] Further details of the grindstones are given in Smith (2004).

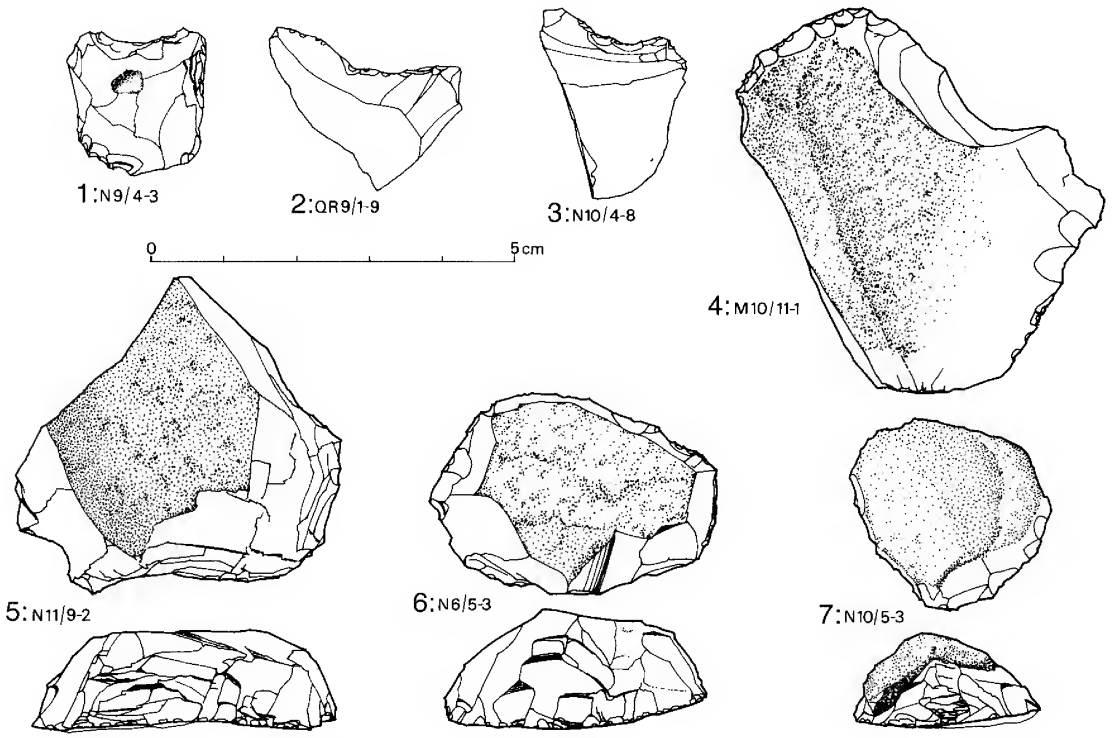

Fig. 17. Retouched artefacts from the Holocene levels of Puritjarra rock shelter. All are from units 1a and 1b except M10/11-1 (unit 1c). Steep-edged scrapers: N11/9-2, N6/5-3, N10/5-3. Notched implements: N9/4-3, QR9/1-9, N10/4-8. Endscraper: M10/11-1.

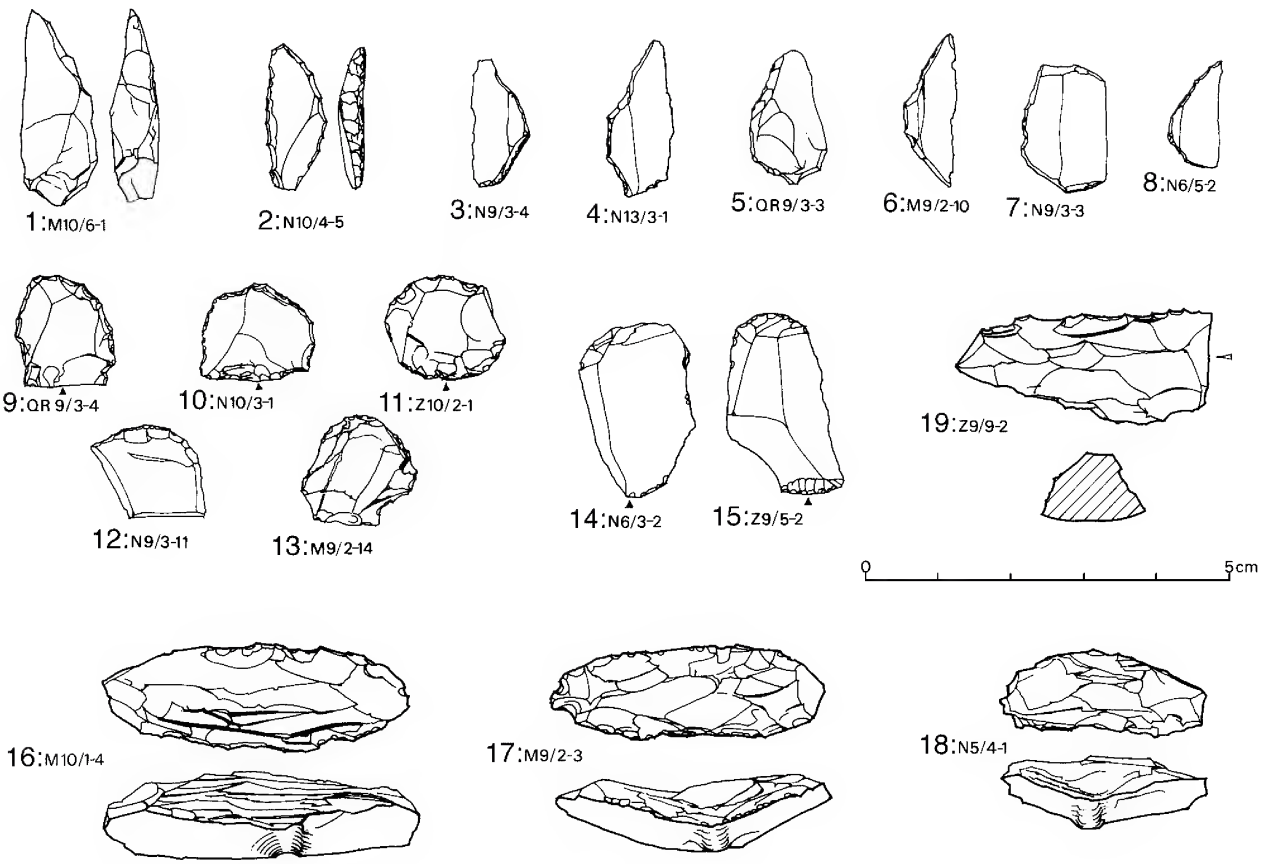

Fig. 18. Group 2 retouched artefacts from the Holocene levels of Puritjarra rock shelter. All are from units 1a and 1b. Geometric microliths: top row (1–8). Thumbnail scrapers: QR9/3-4, N10/3-1, Z10/2-1, N9/3-11, M9/2-14. Tula adze slugs: M10/1-4, M9/2-3, N5/4-1. (M10/1-4 is the largest tula in this assemblage). Burren adze slug: Z9/9-2. Endscrapers: N6/3-2, Z9/5-2. (Z9/5-2 has use-polish and rounding on the distal end, and fine overhang removal scars along the platform edge).

Table 13. Correlation matrix for tool types. Data are raw counts of each tool type per spit (excavation unit); n = 336 spits. This correlation matrix was generated as part of a Principal Components Analysis using the MV-ARCH program.

	Tula slugs	Thumb-nail scrapers	End-scrapers	Steep-edged scrapers	Notched tools	Saws	Amorphous retouched implements
Geometric microliths	0.38	0.32	0.24	0.13	0.04	-0.05	0.11
Tula adze slugs	—	0.27	0.24	0.17	0.18	-0.03	0.35
Thumbnail scrapers		—	0.21	0.09	0.03	-0.05	0.33
Endscrapers			—	0.13	-0.07	-0.08	0.09
Steep-edged scrapers				—	0.24	0.10	0.22
Notched tools					—	-0.05	0.21
Saws						—	-0.07
Amorphous retouched implements							—

thumbnail scrapers are best known from late Holocene assemblages, although these implements occur in late Pleistocene contexts in Tasmania (Holdaway, 2004).

Endscrapers. These are long flakes with a convex retouched edge on the distal end (cf. O'Connell, 1974, 1977: fig. 4g,h). Retouch ranges from finely invasive fluting to smooth step-flaking on the steeper edges. These implements are made on a variety of stone, but sandstone and silcrete were the most commonly used materials (71%). They may be a hand-held version of thumbnail scrapers. Like thumbnail scrapers, some endscrapers have a well-developed use-polish with striations running transverse to the edge (N6/3-2, Z9/5-2) (Figs 18.14, 18.15). Although their archaeological distribution is patchy, endscrapers have been recovered in excavations elsewhere in central Australia, at Puntutjarpa rock shelter (Gould, 1977: fig. 58) and Intirtekwerle (Gould, 1978: figs. 8c, 13; Smith, 1988: 230) and on open sites in the Sandover River region (O'Connell, 1977: fig. 4g,h). The function of these implements is not known but they may be a smaller version of the ethnographic implements known as "yilugwa" or "alywek" in Alyawarr, which were used as spoons and scrapers for preparing and consuming fibrous roots and tubers (O'Connell, 1974).

Table 14. Attributes of retouched artefacts. Data are for complete implements unless indicated.

Amorphous retouched implements

analytical unit	n	wt g	length mm	retouch L mm	l/b ratio[e]	>1 retouched edge %	% broken implements[f]
1a	103	16±34	31±16	25±15	1.3	12	15
1b	53	25±66	12	—	—	—	—
1c	24	30±36	—	14	—	—	—
2a	43	55±52	53±18	41±22	1.3	19	8
2b	0	—	—	—	—	—	—
2c	1	9	43	24	2.0	—	—

Steep-edged scrapers

analytical unit	n	wt g	length mm	retouch L mm	edge angle	>1 retouched edge	% broken implements[f]
1a	20	14±20	29±12	23±8	80	25	29
1b	10	18±17	31±8	28±11	77	20	9
1c	4	31±26	—	20	—	—	—
2a	14	136±204	64±35	43±32	71	57	—
2b	1	333	86	60	85	—	—

Notched implements

analytical unit	n	wt g	length mm	notch width mm	notch depth mm	>1 retouched edge[g]	% broken implements[f]
1a	14	7±6	29±10	11±5	2±1	29	—
1b	4	3±2	24±4	11±2	2±0	—	—
1c	—	—	—	—	—	—	—
2a	5	19±16	44±13	13±4	4±2	—	17

[e] Complete implements on flakes only.
[f] Artefacts where a section of retouch is truncated by a break. Calculated as percentage number of all of tools of this type in each unit.
[g] These artefacts have a retouched edge in addition to a notch. Only one implement has a second notch.

Temporal relationships of Group 2 implements. Although backed artefacts are known to occur in early Holocene contexts (Hiscock & Attenbrow, 1998), geometric microliths only make up a significant component of assemblages in south-eastern Australia after 4,000 B.P., spreading across the southern two thirds of the continent over the next millennium. At Puritjarra, the major distribution of geometric microliths, tula adze slugs and thumbnail scrapers is within the upper 25–30 cm of the deposit (units 1a and 1b, <3,500 B.P.) but neither are common until c. 2,000 B.P. A single small geometric microlith on chalcedony (weighing only 0.2 g) (N6/15-1) was recovered from the middle of unit 1c, where it would date to about 5,500 B.P. This conforms to the size and elongate form of the microliths in 1b. There is no sign of disturbance in this part of the site but, given its small size, the artefact may have been accidentally displaced from a higher level during excavation. Alternatively, microliths may have been occasionally produced in the mid Holocene.

Despite its long sequence, Puritjarra leaves the history of one of the most distinctive desert technologies unresolved. The combination of *Triodia* resin (as a hafting cement) with a specialized adze-morphology (the tula adze flake) is thought to be an adaptation specifically for working desert hardwoods (Sheridan, 1979). The earliest known tula slugs date to 3,500 B.P. at Devon Downs rock shelter in the lower Murray valley, and at the central Australian site of Kwerlpe, just above a radiocarbon date of 3,635±90 B.P. (I-7602) (Gould, 1978; Smith, 1988: 236). At Puritjarra, tula adzes appear abruptly in the sequence, with other Group 2 implements, without any indication of the history of development of these implements (the earliest examples are N5/7-5 and N5/7-6 from unit 1b which date to between 800 B.P. and 3,500 B.P.). A re-analysis of adzes from Puntutjarpa rock shelter in the Western Desert (Hiscock & Veth, 1991) came to similar conclusions, dismissing Gould's argument that there was a 10,000-year sequence for desert adzes at this site (Gould, 1977).

Regarding the origin of Group 2 implements, Hiscock (1994) argued that high-levels of residential mobility, and the need for a portable multi-functional tool-kit, underlay widespread use of these implements in the late Holocene. Whatever the case, the increased use of thermoplastics (such as *Triodia* resin) as hafting cement was the proximal cause

of much of the variability in the late Holocene tool kit. First, it brought lithics into closer articulation with the wooden toolkit (as stone components or bits in wooden composite tools) where much of the functional variability in desert material culture is manifested (cf. Peterson, 1971). Secondly, we could expect new hafting methods to have a wide impact on a stone artefact assemblage (Keeley, 1982). At Puritjarra, we can see this not only in the appearance of Group 2 implements, but also in changes in the use and breakage of other implement types after 3,500 B.P., such as steep-edged scrapers and notched implements.

Other retouched or utilized artefacts

The common feature of the artefacts in this group is that they are products of the use and resharpening of implements.

Amorphous retouched artefacts. These are artefacts with a short length of retouch on one or more edges but with little modification of the overall form of the implement or the working edge. Most have evidence of only light trimming, resharpening or utilization. Few would be typologically classifiable as scrapers (only 9%, including M10/22-2, M11/18-1, N11/19-3) (Figs 15.2, 16.7, 16.8). The majority are made on flakes (84%). In units 1a and 1b these blanks were slightly thicker on average than unmodified flakes at the same level but are otherwise similar in size and shape. This is not the case in unit 2a where flakes >50 mm long were often selected for use as implements (e.g., M10/22-2, Fig. 15.2). As with other implement types, there is greater use of chert and chalcedony over time, as well as a progressive reduction in the size of these implements (Table 14). Breakage rates for artefacts in units 1a–c are also higher than those for unit 2a. Ethno-archaeological studies suggest that the major use of secondary retouch was to resharpen or rejuvenate a dulled working edge (Hayden, 1977: 179–180).

Retouched fragments and trimming flakes. Some of these artefacts are fragments of broken tools. Others, especially those in units 2a–c, are trimming or resharpening flakes off a retouched edge (M11/27-4, M11/23-7, N13/14-6). In units 2a–c materials such as grey silcrete and chalcedony are over-represented amongst trimming flakes, compared to implements. This suggests that tools of higher-grade stone were more extensively curated or recycled than those of local materials. Within the Holocene most of the artefacts in this category are broken ends or projections off retouched implements rather than trimming flakes.

Artefacts with use-polish. Throughout the Puritjarra assemblage there are a small number of artefacts with use-polish, fine abrasion and rounding of an edge (e.g., N13/18-16, N13/16-4). Sometimes this takes the form of a distinct bevel with striations transverse to the edge. It is often found on silcrete artefacts but is not restricted to one type of implement and is present on the chord of a geometric microlith (N9/3-3, Fig. 18.7), the edge of a tula slug (N11/2-3), on thumbnail scrapers, endscrapers, and on unretouched flakes. It is similar to the polish on ethnographic implements known as yilugwa, used as spoons and scrapers for fibrous roots and tubers (O'Connell, 1974).

Use and reduction of tools

Possible function of large implements in late glacial levels. The artefacts in unit 2a are extraordinarily large compared to those earlier in the late Pleistocene (units 2b–d), or in the mid-late Holocene (units 1a–c). Fig. 14 shows the extent of this trend, where the mean weight of lithics per spit in unit 2a (85–105 cm below datum) often falls in the range 10–40 g, in contrast to units 1a–c and 2b–d where mean weight of lithics per spit is generally less than 5.0 g. The implements in unit 2a contribute to this trend, with a mean weight of 75±127 g (unit 2a, all complete retouched artefacts, N = 62) compared to 13±34 g for units 1a–c (all complete retouched artefacts, N = 386).

Large flake or block implements, such as those found in unit 2a, probably served as expedient heavy-duty woodworking tools. However, microscopic examination of the edges of several tools for organic residues was inconclusive. Many flaked stone artefacts and grindstones at Puritjarra are covered with starch grains, especially acacia starch. This was also the case with the large flake implements examined (QR9/8-1, M10/22-2, N10/9-1) (Figs 15.1, 15.2, 16.9). Other work shows that starch occurs naturally in the rock shelter sediments (Bowdery, 1998; Smith, 2004: 179–180), often in appreciable quantities (>500 grains/mm^2 on non-cultural control samples), and may derive from deflation of inter-dunal soils beneath acacia groves upwind of the site.

The two functions which require a large artefact mass are heavy-duty woodworking (chopping or scraping) and use as a core. Artefacts identified as amorphous implements or saws are unlikely to be confused with cores. However, the question often arises as to whether steep-edged scrapers are cores rather than implements (Holdaway & Stern, 2004: 37–40, 204, 243–244). At Puritjarra these artefacts do not appear to reflect flake production. Most appear to be implements, since flaking is generally limited to their edges. Most flake scars are <10 mm long and the majority are shallow step-fractures suggestive of use damage rather than deliberate flake removals.

The ratio of unmodified flakes to cores offers some support for this interpretation (Table 15). Systematic misclassification of cores as tools would inflate flake/core ratios (by taking many cores out of the equation). However, flake/core ratios for unit 2a are very low compared to units 1a–c and 2b (the opposite of what we would expect if a significant number of cores were misclassified as tools). There are two alternative interpretations of this pattern: the steep-edged scrapers in 2a reflect repeated unsuccessful flaking or testing of sandstone blocks, or that blocks of stone were opportunistically used as implements and sometimes trimmed or resharpened during use. The latter seems more likely, especially given the other evidence for use of large flakes and large implements in unit 2a (Fig. 14).

Organic residues on chalcedony artefacts. Examination of artefacts for residues showed that chalcedony artefacts from unit 1a sometimes have a dark greasy film on their surfaces. The film on M11/3-5, a thumbnail scraper, was tested with hemastix and gave a strong positive (+++) reaction both with and without EDTA buffering, suggesting that this material is blood or animal grease. These residues do not appear to be restricted to a particular category of artefact, or to be limited to the edges of artefacts. Therefore,

Table 15. Flake:core ratios. Data are number of unmodified flakes relative to number of cores—for each raw material category.

analytical unit	all materials	silicified sand-stone	white chalcedony
1a	29	25	42
1b	38	39	33
1c	29	31	39
2a	11	8	13
2b	38	18	no cores

they may reflect the general context of use (spillage of blood and grease during food preparation nearby, greasy hands, etc.) rather than the primary function of these artefacts.

GIR and PRI for retouched flakes. Law (2003) has applied two reduction indices to retouched flakes in the Puritjarra assemblages (Table 16): the geometric index of reduction (GIR or GUIR) described by Kuhn (1990), and a perimeter reduction index (PRI) adapted from Barton (1988). GIR provides a measure of edge-thickness relative to flake-thickness, and interpolates the extent to which a lateral edge has been worked back towards the mid-line of the flake. Its major limitation is that it is only applicable to dorsally retouched flakes with a trigonal cross-section. The PRI is a simple measure of retouch length as a proportion of total edge-length on a complete flake. Although most of the samples in Law's study are too small (N <30) to reliably estimate population means and variance, several trends are suggested by his data. Flake tools are more heavily trimmed or resharpened in unit 1a and 1b compared to earlier levels, and this shift largely reflects more intensive reduction of stone from distant sources (50–100 km from Puritjarra) (Table 16a). Similarly, there is more extensive retouching of flake margins during unit 1a (Table 16b), and this also mainly involves stone from distant sources. Both trends are consistent with more intensive use of the rock shelter in the late Holocene, given that this is likely to have involved a greater range of on-site repair and maintenance tasks, as well as pressure to economize on the use of exotic stone by resharpening tools as much as possible (cf. Holdaway & Stern, 2004: 80).

Continuity and change in flaked stone industry

In archaeological nomenclature, a stone "industry" is a group of assemblages which reflect the operation of distinctive flaking or production methods, or are made on specific raw materials (e.g., quartz), or have a distinctive tool inventory (cf. Holdaway & Stern, 2004: 18). The premise is that a common technology will create similarities between assemblages irrespective of any variability created by local circumstances. In Europe and southern Africa, archaeological systematics provide much of the structure for regional prehistory. In Australia, where patterns of site use, mobility and logistics appear to be the major factors in inter-assemblage variability, it has been difficult to identify discrete stone industries (see Holdaway, 1995 for a discussion). In the Puritjarra sequence, there is little evidence to suggest that there was any significant change in flaked stone industry throughout the occupation of this site.

Flaking methods and core preparation. These remain broadly similar throughout occupation of the rock shelter, producing squarish flakes of variable size, from lightly prepared cores. The long-term trend towards smaller flakes and cores at this site, reflects more intensive core reduction, together with increasing use of cherts and chalcedony, rather than changes in flaking methods.

Shifts in raw material. The shift from silcrete-dominated assemblages in the late Pleistocene, to chert/chalcedony-dominated assemblages in the mid-late Holocene, appears to be a local rather than regional change. It is not evident at Kulpi Mara (Thorley, 1998b: 236) or at Puntutjarpa (Gould, 1977). Nor are chert and chalcedony invariably associated with small-tool phase assemblages in central Australia. The dominant raw material in late Holocene contexts is fine-grained silcrete (Gould, 1978; Smith, 1988). Of Group 2 implements, only tula adzes show strong preference for chert or chalcedony.

Changes in typology. These are limited to the late Holocene when small-tool phase (Group 2) implements appear in the Puritjarra sequence, about 3,000–3,500 B.P. (or possibly earlier if the geometric microlith in level 1c is accepted as in-situ), together with the earliest seed-grinders at this site (Smith, 2004). In the desert, Hamilton (1980) describes the ethnographic differentiation of tool kits into specialized men's (hafted

Table 16. Variation in flake retouch, after Law (2003, chapter 6).

	all materials		local stone		transported stone (50–100 km)	
analytical unit*	n	mean	n	mean	n	mean
(*a*) **Geometric index of flake reduction (GIR)**						
1a	55	0.42±0.18	19	0.34±0.11	18	0.46±0.21
1b	43	0.50±0.27	9	0.28±0.14	18	0.60±0.25
1c	15	0.39±0.14	11	0.40±0.15	3	0.32±0.12
2a	17	0.32±0.16	17	0.32±0.16	—	—
all units combined	130	0.43±0.21	56	0.34±0.14	39	0.51±0.24
(*b*) **Perimeter reduction index (PRI)**						
1a	132	0.41±0.21	47	0.33±0.18	50	0.43±0.21
1b	87	0.37±0.21	26	0.31±0.22	37	0.41±0.25
1c	29	0.37±0.18	20	0.38±0.19	8	0.37±0.12
2a	40	0.36±0.17	36	0.36±0.16	3	0.55±0.11
all units combined	288	0.38±0.20	129	0.34±0.18	98	0.42±0.18

* Law's study arbitrarily divides "unassigned layer I" material between units 1b and 1c and may obscure some differences between these units.

adzes and composite spears) and women's (seed grinding implements) equipment. If the appearance of Group 2 implements and seedgrinders can be taken as an archaeological correlate of this, it suggests that men's and women's roles became more strongly delineated after 3,500 B.P.

Earlier changes, towards the use of large flake and block implements in unit 2a, may reflect shifts in site function rather than typology, as these implements are found in lower frequencies throughout the late Pleistocene (unit 2b) and mid-Holocene (unit 1c) levels of the site. In this sense, the large core and flake artefacts in unit 2a would constitute a "facies" rather than an industry. Large block and flake artefacts have not been reported from terminal Pleistocene/early Holocene contexts elsewhere in central Australia—see Kulpi Mara (Thorley, 1998a,b); Puntutjarpa (Gould, 1977); and Serpent's Glen (O'Connor *et al.*, 1998)—but do occur at Hawker Lagoon and Balcoracana Creek in northern South Australia (Lampert & Hughes, 1988).

Characterising site use

We can work back from the economics of stone usage to reconstruct how sites such as Puritjarra articulated with a cultural landscape. Archaeologists, argues Binford, tend to see the past from the perspective of fixed positions in space. "The 'fallout' from the events that 'moved across' fixed places establishes the character of the archaeological remains on sites" (1982: 6). He suggests we image ourselves as observers at the bottom of a site "looking up as the dynamics of human systems pass over" (Binford, 1982: 20), emphasizing the potential to use sites like Puritjarra to provide a window on a wider cultural or economic landscape. Like similar studies (e.g., Cundy, 1990; Holdaway, 2004; Veth, 1993), the premise in this paper is that the strategies people adopted for acquiring, using and discarding stone, were embedded in a broader system of land use.

Table 17. Changes in intensity of occupation.

(*a*) Quantitative indicators

analytical unit	lithics no./10 kg[e]	cores no.	grind-stones no.	ochre no.	charcoal g/10 kg[e]	emu egg-shell wt. g	bone wt. g	pits and hearths no.
1a	48.6	34	49	33	5.21	12.6	62.6	10
1b	27.0	14	11	13	0.28	0.9	50.9	3
1c	14.0	11	8	29	0.01	—	2.0	3
2a	2.2	39	4	63	0.11	—	—	4
2b–d	<0.1	3	1	58	<0.01	—	—	—

[e] Relative to weight of excavated sediment.

(*b*) Estimated artefact discard rates

analytical unit	time period yrs B.P.	artefacts[f] no./100 yr	area excavated[g] %	estimated discard rates[h] no./100 yr
1a	0–800	903	3.5	25800
1b	800–3,500	201	3.3	6090
1c	3,500–7,500	59	3.3	1790
2a	7,500–18,000	17	3.0	570
2b–d	18,000–33,000	2	4.5	45

[f] Excavated trenches only.
[g] Of floor area available during each period.
[h] Interpolated for entire deposit.

(*c*) Other indices

analytical unit	reduction	breakage rates			tool inventory		exotic materials	
	retouched flakes (GIR)[i]	cores and tools %	flakes (L)[j] %	flakes (T)[k] %	richness[l]	diversity[m]	stone[n]	ochres[o]
1a	0.42	25	9	14	5.63	1.95	0.64	0.70
1b	0.50	31	8	22	4.80	1.74	0.67	0.62
1c	0.39	27	6	17	3.69	1.04	0.26	0.41
2a	0.32	18	6	2	4.19	1.32	0.26	0.59
2b–d	—	22	9	1	1.10	1.39	0.23	0.93

[i] Geometric Index of Reduction. Data from Law (2003).
[j] Longitudinal breaks.
[k] Transverse snaps or breaks.
[l] Richness is number of tool types/log(sample size).
[m] Shannon-Weaver diversity index (H) using data in Table 12, but excluding retouched fragments, trimming flakes and redirectors.
[n] Ratio by number of exotic:local stone, using data in Table 5. Exotic stone is stone from sources 50–100 km from Puritjarra.
[o] Ratio by number of exotic ochre (from sources 50–100 km from Puritjarra) to other ochres.

A wide range of indicators are commonly used to characterize the nature of occupation at a site: quantitative measures of occupation intensity including artefact discard rates; patterns of artefact breakage and recycling; indices of assemblage richness and diversity; flake reduction indices including GIR, PRI and flake/core or flake/tool ratios; and various proxy measures of residential mobility (for recent examples see Barton, 2003; Elston, 1990; Holdaway, 2000).

Tables 17 and, 19 summarize site use indicators for each analytical unit at Puritjarra. Some caveats need to be borne in mind in interpreting these indicators:

Behavioural correlates. Hiscock (1981) pointed out that general measures of "intensity of site usage" conflate different sorts of behaviour and that it is crucial to separate these during analysis.

Mix of occupation events. Analytical units will generally be a mix of different types of occupation event (each with a range of behaviours). Many occupation deposits represent palimpsests, involving a long-term process of accumulation, multiple occupation episodes, and a mix of short-term and extended-stay visits, with varying site inventories and patterns of residential mobility (cf. Barton, 2003). It follows that analytical units are unlikely to have direct analogues in ethnographic site types.

Shifts in archaeological signature. Binford reminds us that "humans may reposition their adaptive strategies in a landscape, a tactic which may generate variability in the archaeological record while serving to foster stability within the ongoing system" (1982: 6). Changes in the archaeological signature of a site (a composite of different types of occupation event) may reflect changes in the role of that site in a cultural landscape, rather than systemic changes in population, land use or subsistence.

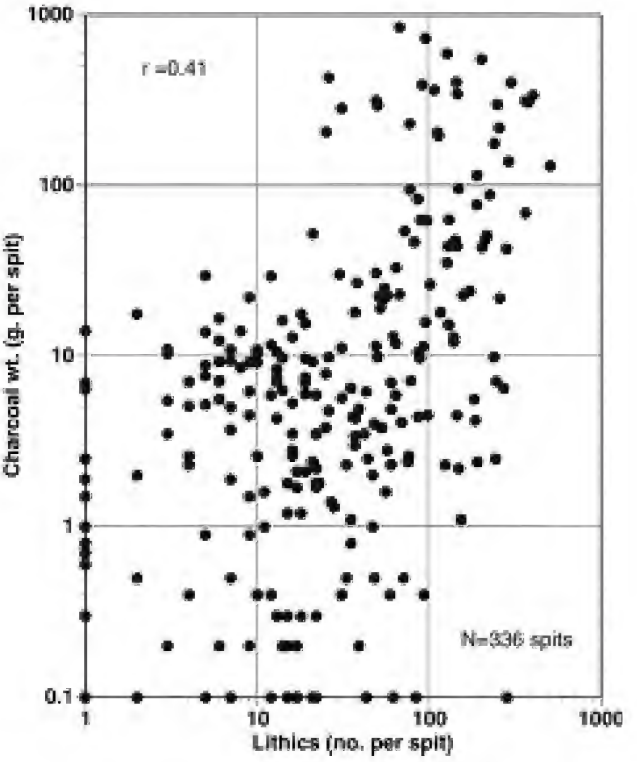

Fig. 19. Graph showing relationship between amount of charcoal and number of chipped stone artefacts in excavation units. Data are plotted for all spits (N=336). There is broad agreement between the two measures of occupational intensity (r=0.41).

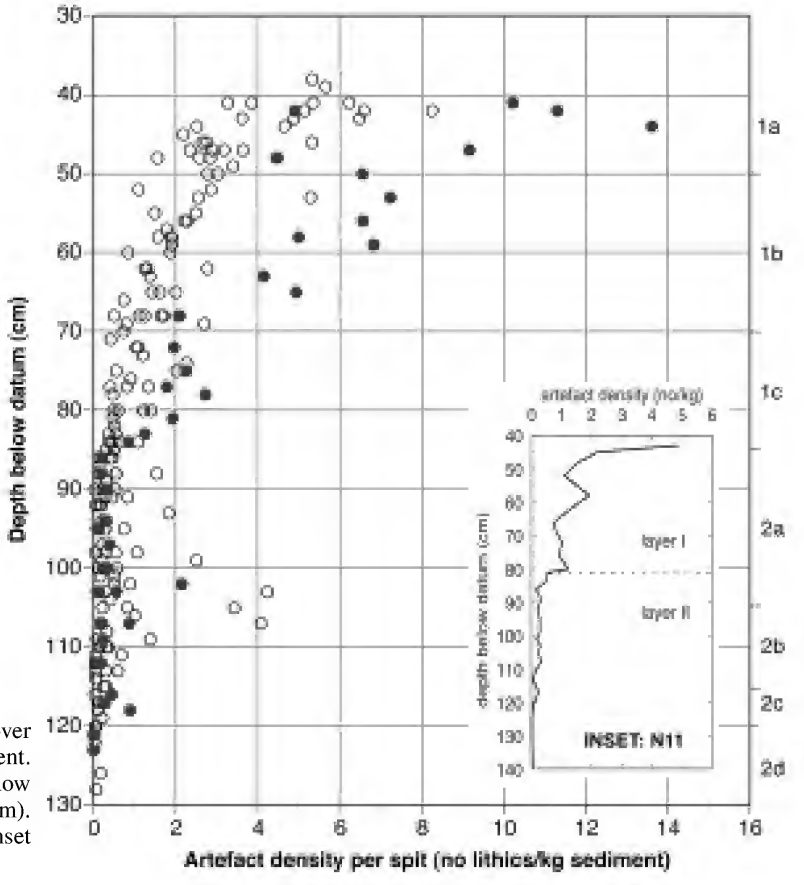

Fig. 20. Changes in the concentration of artefacts over time. Data are number of lithics per spit per kg sediment. Open circles are artefacts >6 mm. Solid circles show corresponding figures for fine flaking debitage (3-6mm). Plot shows data for the Main Trench (N=168 spits). Inset shows trend in grid square N11.

Table 18. Spatial distribution of artefacts.

analytical unit	rear wall N sector	rear wall rock fall zone	central floor N sector	central floor rock fall zone	central floor S sector	dripline
(*a*) Total number of artefacts						
1a	541	121	4616	714	1111	124
1b and 1c[1]	983	1072	3930	537	1145	111
2a[2]	297	79	657	105	541	64
2b[3]	1	—	235	—	17	4
2c	—	—	41	—	—	1
2d[4]	—	—	16	—	—	—
(*b*) Frequency by unit (%)						
1a	7	2	64	10	15	2
1b and 1c[1]	13	14	50	7	15	1
2a[2]	17	4	38	6	31	4
2b[3]	<1	—	91	—	7	1
2c	—	—	98	—	—	2
2d[4]	—	—	100	—	—	—
(*c*) Average weight (g)						
1a	2.7	10.1	1.5	4.0	1.8	12.2
1b and 1c[1]	5.0	8.7	2.2	4.0	3.1	13.2
2a[2]	25.7	13.4	21.6	25.8	5.5	20.6
2b[3]	2.6	—	6.6	—	1.7	0.9
2c	—	—	5.9	—	—	0.8
2d[4]	—	—	2.5	—	—	—

1 Combined here with "unassigned layer I" to allow coverage of zones across the shelter floor.
2 Includes data from selected spits in "unassigned layer II": ST5/8-ST5/10, N10/7 and QR9/6.
3 Combined with remaining "unassigned layer II": N5/26, Z9/39 and Z10/9–Z10/10.
4 One core (M10/28-1) and five flakes (from N5/27, N11/35 and N12/31) are doubtful artefacts and are omitted.

Artefact deposition: densities and rates

The quantitative indicators in Table 17a show that Puritjarra rock shelter was used progressively more intensively over time—with the heaviest use of the site during the last 800 years (unit 1a). There is broad agreement between artefact discard rates (Table 17b) and changes in other occupational debris, such as the number of grindstones, frequency of pits and fireplaces, patterns of artefact breakage and reduction (Table 17c), and the concentration of charcoal in the deposit (Fig. 19).

Deposition of flaked stone artefacts was <0.5 artefacts/kg sediment throughout units 2a–d, increasing to 1.5 artefacts/kg in units 1b–c, and increasing again in unit 1a from 2.5 to >5 artefacts/kg (Fig. 20). The overall trend is towards higher concentrations of artefacts in the Holocene levels after c. 7,500 B.P. (Layer I) (80–82 cm). The distribution of fine flaking debitage (3–6 mm) shows a similar pattern to the larger artefacts (>6 mm) (Fig. 20) but concentrations of fine debitage are consistently higher than rates for larger artefacts. The two distributions begin to diverge in unit 1c as chert and chalcedony are more frequently used. In part, this reflects the higher visibility of these materials during sorting of the fine fraction.

Table 17b provides estimated artefact discard rates for each unit taking into account that the excavation trenches represent <5% of the floor area of the rock shelter. Hayden, who studied stone tool use amongst Pintupi people in the area immediately west of the Cleland Hills in 1971, calculated that a family in the Western Desert would use around 150±50 retouched artefacts per year and about the same number of unmodified flakes utilized as tools (Hayden, 1977: 273–274, see also Hayden, 1979: 165–166). Comparing these estimates with the Puritjarra assemblage suggests that unit 1a represents the long-term equivalent of use of the rock shelter by a nuclear family for about 3–6 weeks each year (based on 11–12 retouched artefacts/site/year). Such calculations are speculative, but seem the right order of magnitude given the duration for ethnographic camps in this region. Earlier levels must represent more ephemeral use of the rock shelter, but the diversification of tool-kits after 3,500 B.P. means that Hayden's figures cannot be directly applied to earlier assemblages.

Artefact concentrations are very variable during the late Pleistocene (2a–d) reflecting intermittent use of the rock shelter at this time. There is a localized concentration of artefacts at levels dated to the last glacial maximum (105 cm below datum) suggesting there was greater use of the rock shelter at this time (Figs 20 and 21).

Assemblage diversity and richness

Residential base-camps are locations where we could expect the widest of range of subsistence activities, tool production and repair, as well as extended residence—and hence the largest and most diverse artefact assemblages (Shott, 1986). On a multi-decadal timescale, repeated use of such central locations—involving long and short-stay visits, groups of varying composition, and occupation during different times of the year—is likely to reinforce a pattern of relatively dense

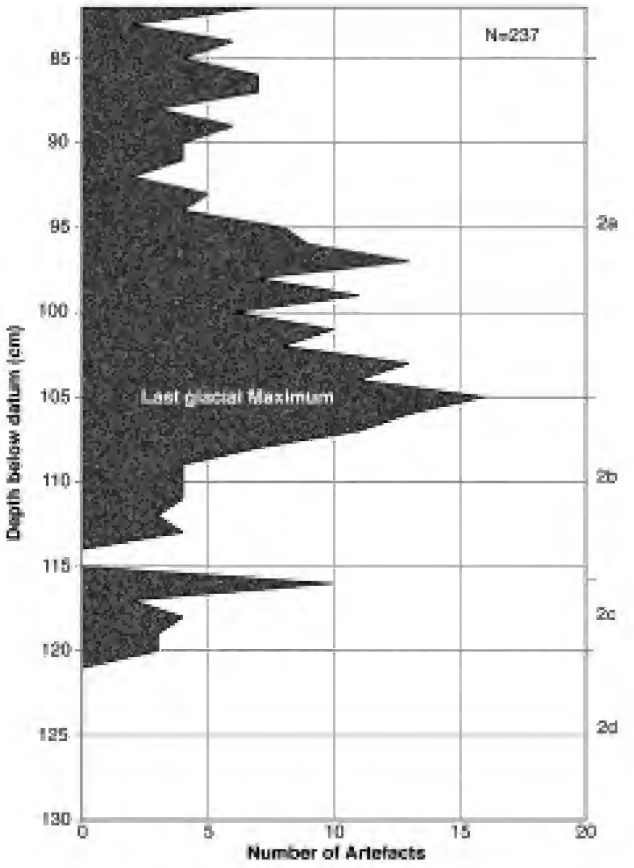

Fig. 21. Fine-grained vertical distribution of artefacts in late Pleistocene sediments (units 2a–d). Data are number of levelled finds (artefacts for which the precise depth was recorded in-situ during excavation) per cm depth in the Main Trench. The plot shows the concentration of artefacts on the palaeosurface at c. 32000 B.P., and a peak in artefact numbers coinciding with the last glacial maximum.

and coarse-grained assemblages (as Veth, 1993: 82 found for core occupation sites near water in the Great Sandy Desert).

Table 17c gives estimates of assemblage diversity and richness for the Puritjarra occupations. Following Odum (1971: 144), *richness* is number of tool types/log (sample size), and *diversity* is the Shannon-Weaver diversity index (H') (Odum, 1971: 144). Richness is standardized against log(sample size) to remove the effect of sample size on number of tool types. The results in Table 17c show that site inventories (richness) increase over time, with unit 1a being noticeably richer than other units. Similarly, diversity increases over time, and unit 1a has the most diverse assemblage. Both indices identify unit 1c as an anomaly in this trend, with a more limited site inventory.

Barton (2003: table 5) includes comparative data for open sites in the Simpson Desert. Values for unit 1a are comparable to those for residential base camps, near springs in the Simpson Desert (richness 5.44; diversity 1.58). Site inventories in units 2b–d are conspicuously poorer than anything in Barton's sample. Veth (2005a: table 6.6) provides figures for artefact diversity on Western Desert sites (8.0 for base camps; 4.0 for ephemeral residential camps; 2.0 for task specific sites). These figures are higher than in any unit at Puritjarra, but may not be strictly comparable: That they are so much higher than those in the Simpson Desert sample, may indicate he has used a different algorithm to calculate "diversity".

Breakage patterns

Transverse snapping of flakes is generally taken as an indicator of the intensity of treadage on a surface, prior to burial of the flakes (Holdaway & Stern, 2004: 114). Longitudinal breaks or splits in flakes tend to derive from problems during knapping. At Puritjarra, the higher incidence of transverse breaks in layer I (units 1a–c) (Table 17c), despite the higher rate of sediment accumulation in this layer, indicates more intensive use of the rock shelter after 7,500 B.P. Breakage patterns for tools and cores (Table 17c) show a similar pattern (though these indicate breakage during use). The incidence of longitudinal breaks shows less variability—much as we might expect, given there is little change in flaking methods during the history of the shelter.

Spatial patterns

Spatial patterns in archaeological remains at different levels confirm the picture of progressively more intensive use of the rock shelter over time. People using a campsite for any length of time tend to clear living surfaces and heavily trafficked areas of large debris. Larger items often end up on talus slopes outside a rock shelter or along the drip-line at the edge of the overhang. At Puritjarra, the general pattern was that larger rocks and artefacts were discarded along the drip-line and also around the large boulders that divide the central area of the rock shelter floor into northern and southern sectors (Table 18). Artefacts left on the main living floor average only a few grams. This pattern was not established until c. 7,500 B.P., coinciding with other evidence for more intensive use of the shelter during the mid-late Holocene (units 1a–c).

When people first used Puritjarra, the major rock-free floor was the northern sector of the shelter. Occupation of the rock shelter at the time units 2b and 2c were accumulating was limited to the central part of this floor and most artefacts appear to have been left where they were used or produced.

During unit 2a occupation extended across all zones of the rock shelter, from the rear wall out to the drip-line, and included both northern and southern sectors of the floor. At least one hearth in the central of the floor is associated with this horizon (dated by M10/20-4, 9,110±120 B.P. ANU 6538). Towards the rear wall a small pit (N5/25) was dug about 13,000 B.P. and rapidly filled with sediment leaving a shallow depression in which debris of various sorts subsequently accumulated, including cores, large flake implements and a large tablet of red ochre. However, there was little size sorting of debris at this time, except perhaps on the southern floor: large artefacts were usually left on living surfaces. This indicates that most visits were still relatively short.

The modern pattern was established during unit 1c: larger debris was routinely cleared from the central floor of the rock shelter. Larger rocks, cores and broken grindstones accumulated around fallen boulders and between these boulders and the rear wall of the rock shelter. A range of pits and fireplaces are associated with unit 1a, and intact grinding slabs are sometimes associated with small ashy lenses in this unit.

Mobility indicators

Changes in intensity of site usage can be broken down into a number of components: changes in group size; changes in the duration of visits; or changes in the frequency of visits. Behr (1990) and Law (2003) have attempted to "unpack" the trend towards more intensive use of Puritjarra rock shelter during the last millennium. Both studies suggested that increased residential mobility was involved in this shift (i.e. more frequent visits to the rock shelter), based on increased use of white chalcedony at this time.

Table 19 gives various measures of relative mobility for the Puritjarra assemblages. The premise underlying such indicators is that highly mobile groups generate assemblages with the highest proportion of exotic raw materials, but only small numbers of tools, whereas less mobile groups make greater use of local stone, more intensively use and recycle any exotic stone available, and generate more diverse site inventories (see Holdaway & Stern, 2004: 80 for a discussion).

At Puritjarra, the most diverse tool inventories and greatest reduction of white chalcedony occur in unit 1a. This unit also has the lowest flake/tool ratio, indicating that a relatively high proportion of chalcedony flakes have been transformed into tools (complementing GIR and PRI indices showing greater resharpening of chalcedony flakes in this unit). High flake/core ratios can indicate either (a) greater reduction of cores, or (b) their systematic removal from the site by mobile groups (cf. Holdaway, 2000: 223). At Puritjarra, the evidence is more consistent with increasing reduction of cores, together with a trend towards a reduction in chalcedony flake length over time (though this is not statistically significant), and an overall reduction in the weight of white chalcedony artefacts. These indicators point to extended occupation of the rock shelter in unit 1a, confirming the pattern shown by artefact discard rates and changes in other occupational debris.

Against this trend, the high proportion of exotic stone and ochre in unit 1a is an anomaly. It could reflect a switch in provisioning strategy, from "embedded" procurement of stone and ochre (Holdaway & Stern, 2004: 80) to a logistical pattern of direct procurement, as use of the rock shelter intensified. However, I think it more likely that unit 1a is a mix of extended and short-term occupations involving more frequent cycling of people through the shelter. Veth (1993) describes a "dual" system of seasonally occupied core occupation sites and satellite camps for the Martutjara in the Great Sandy Desert. It is relevant that residential base camps in the Great Sandy Desert also have high frequencies of non-local stone (62%) (Veth, 1993: table 4.2), combining this with heavy reduction of exotic stone.

Table 19 ranks analytical units against each mobility indicator, and sums rank-order scores to produce an index of relative mobility. The results show a decline in overall residential mobility over time—irrespective of any changes in the "mix" of occupations in these units.

Discussion

History of the rock shelter

The archaeological evidence suggests a series of phase shifts in the character of occupation at Puritjarra. Although each of these phases must represent a palimpsest of numerous small camps and a mix of debris from different tasks, functions and activities, the cumulative archaeological signature is different in each phase. The pattern of occupation in units 1c, 2a and 2b–c could be seen as variants of the one system—scaled by task and intensity of residential mobility—but even here the changes are sustained and probably represent significant restructuring of land use in the Cleland Hills. The following discussion draws together the various lines of evidence about the nature of occupation in each phase.

Initial visits to the rock shelter

Colonization of the Australian desert may well have been preceded by an exploratory or pioneer phase, involving the dispersal of human groups across the interior (see Smith, 2005b for a discussion). Given that human dispersal across the continent took place before 45,000 years ago (O'Connell & Allen, 2004) and that the northern margins of the desert were settled soon after, we could expect the first movements into the desert in the period 35,000–45,000 years ago, though there is no firm evidence for this at present. At Puritjarra, however, there is some *equivocal* evidence for fleeting human visits prior to occupation at c. 32,000 B.P. (unit 2c). Excavations at the base of layer II (the lower part of unit 2d), recovered a small number of artefacts and possible artefacts in sediments dating to 44.8±3.6 ka (AdTL91010). These include 5 small flakes (an ironstone flake N5/27-1, plus 3 grey silcrete flakes from N11/35 and 1 from N12/31), a large sandstone block with flake scars along both sides of one edge that may be a core (M10/28-1), and a small piece of fine red ochre (0.59 g) from N12/

Table 19. Index of relative mobility. Data are for artefacts on white chalcedony only, except where indicated otherwise. Figures in brackets give rank order by variable.

analytical unit	diversity[e]	flake:tool ratio[f]	flake:core ratio	mean weight lithics (g)	exotic stone[g]	exotic ochre[h]	rank sum	relative mobility[i]
1a	1.95 (1)	1.85 (2)	42 (1)	0.70 (1)	0.64 (3)	0.70 (4)	12	1
1b	1.74 (2)	1.88 (1)	33 (3)	0.72 (2)	0.67 (4)	0.62 (3)	15	2
1c	1.04 (5)	2.79 (4)	39 (2)	0.84 (3)	0.26 (2)	0.41 (1)	17	3
2a	1.32 (4)	2.78 (3)	13 (4)	2.44 (5)	0.26 (2)	0.59 (2)	20	4
2b–d	1.39 (3)	3.00 (5)	no cores (5)	1.55 (4)	0.23 (1)	0.93 (5)	23	5

[e] All raw materials—from Table 17c.
[f] Tools on flake blanks only.
[g] Ratio of exotic:local stone—from Table 17c. Exotic stone includes chalcedony, chert and silcrete.
[h] Ratio of exotic:other ochres—from Table 17c.
[i] Higher values indicate greater mobility.

33. Of these, the ironstone flake and possible core are on local stone and could therefore be chance products of roof-fall. The four silcrete flakes and piece of ochre are related to human activity, but may not be in-situ, as I could find no corroborative evidence of occupation at this level (such as fine flaking debitage or charcoal). It remains a possibility that people visited Puritjarra prior to c. 32,000 B.P., but existing evidence is insufficient to decide the issue one way or another.

Late Pleistocene occupation (units 2b–d)

A pattern of use of the rock shelter was not established until c. 32,000 B.P. (approximately 35,000–36,000 years cal. B.P.), when increasing aridity may have contributed to greater use of sites like Puritjarra (and hence greater archaeological visibility). The first indication of this is a small scatter of silcrete and chalcedony flakes in the upper part of 2d directly beneath the palaeosurface that represents unit 2c. The excavation suggests a pattern of small shifting scatters of artefacts and occupation debris in the central part of the floor at the northern end of the rock shelter. Unit 2c has the most clearly defined of these scatters (Figs 14 and 21) perhaps because there were few artefacts deposited immediately above it. Note that the gap in occupation that can be seen in Fig. 21 is a shift in location within the rock shelter rather than a break in occupation: fine debitage and a small number of artefacts were recovered from the sieves from this level (see also Smith, 1989: fig. 5 and discussion—but note the chronology has been revised). The pattern established in unit 2c—short visits to the rock shelter by small, highly mobile groups—continued throughout unit 2b.

People visiting the rock shelter during the accumulation of units 2b–c were moving over a wide territory lying west of the main central Australian ranges: they acquired red ochre from the Karrku mine, 125 km north west of Puritjarra (Smith *et al.*, 1998) and brought in flakes of fine-grained silcrete probably from the western end of the main range system, and pieces of white chalcedony. They used steep-edged scrapers made of local sandstone but also fine retouched convex scrapers made of grey silcrete from sources in the Cleland Hills. The latter are only represented by the flakes removed from their edges when they were resharpened: these implements appear to have been strongly curated. The paucity of broken tools or cores and the absence of evidence for clearing debris from occupation surfaces suggest that use of the rock shelter was transitory. In particular, in unit 2c the high proportion of artefacts made of exotic silcrete and chalcedony and the relatively low use of local silicified sandstone indicate greater residential mobility than at any other time in the history of the rock shelter.

The last glacial maximum

Research into the chronology and environmental history of layer II over the last 10 years (Bowdery, 1995, 1998; Smith *et al.*, 1997) has more precisely identified the levels which correspond to the last glacial maximum at this site. The trend of the radiocarbon series indicates that a level 105 cm below datum corresponds to the peak of the last glacial maximum. This is directly dated by ANU 6918 (17,980±160 B.P., recently re-dated using ABOX AMS ^{14}C as 20,240±280 B.P., ANUA10010) (Smith *et al.*, 2001), and is cross-referenced to a major decline in shrubs and grasses in the phytolith sequence at this level (Bowdery, 1998), indicating greater aridity at this time.

A peak in the number of artefacts recorded *in-situ* during excavation, coincides with the LGM levels (Fig. 21), suggesting a greater focus at this time on sites near major waterholes. Closer analysis shows that at 105±2 or between 103–107 cm below datum (63–67 cm below surface) there are 145 artefacts: five retouched artefacts, 40 flakes, three cores and 97 pieces of debitage. The three cores include an amorphous core (N13/20-4, 71.4 g) and two platform cores (N13/20-3, 144.2g; M11/24-1, 2112.3 g) all of silicified sandstone. The retouched artefacts include a notched implement (N13/20-1, Fig. 16.6), three amorphous retouched tools (M11/23-2, N11/26-2 and M10/22-2, Fig. 15.2), and a trimming flake removed from the finely retouched edge of a silcrete tool (M11/23-7). The flakes include small flakes of chert and silcrete and large flakes of local silicified sandstone.

These levels also show the greatest reliance on local silicified sandstone of any of the excavated levels (Table 5). Small pieces of red ochre from these levels are sourced to the Karrku ochre mine to the north, and the artefacts include flakes of exotic silcrete ("Other silcrete" in Table 4). This pattern suggests people were still using a wide territory, but were now combining this with occasional extended visits to sites near reliable waters, such as Puritjarra.

Given that resolution of the Pleistocene record at Puritjarra is ±200 years at best, or more realistically ±500 years, there are obvious limits in our ability to identify gaps in occupation of the shelter itself. However, the fact that there is continuity in implement types and flake technology, and in the sources of stone and red ochre reaching the rock shelter across this period, suggests the LGM did not cause any prolonged hiatus in occupation of the region. The main impact appears to have been on the pattern of land use: at Puritjarra, the LGM coincides with the switch from unit 2b to 2a, reflecting a shift in the role of this rock shelter, rather than a change in stone industry.

Thorley (1998a: 43) was understandably sceptical about evidence for use of the shelter during the LGM, commenting that the small number of artefacts in these deposits could have been displaced from younger levels. He pointed out that sporadic, light occupation is contrary to what would be expected for a site near permanent water at this time. Much of this critique was misplaced as it did not take into account revisions to the chronology of the late Pleistocene deposits (Bowdery, 1995; Smith *et al.*, 1997) since the initial reports of the 1980s. These provide a much stronger picture of water-tethered occupation during the LGM.

The terminal Pleistocene (unit 2a)

The most striking change in unit 2a—and the feature that gives this horizon some stratigraphic definition—is the greater emphasis on use of large core or flake tools (mainly steep-edged scrapers, notched implements and amorphous retouched tools) as well as large unmodified flakes. These artefacts are not exclusively on local silicified sandstone: large flakes of chert and silcrete were also brought to the site, though not manufactured on-site. The large implements suggest greater emphasis on heavy-duty woodworking. We can only speculate on the significance of this change. There may have been a more elaborate suite of wooden implements at this time, greater need for the repair and replacement of such items, or perhaps it became increasingly important to "gear up" at sites near permanent water, such as nearby Murantji rock hole. Whatever the explanation, the last glacial maximum appears to have triggered a new pattern of site use.

From c. 12,000–13,000 B.P., a series of changes suggest a switch to a more geographically circumscribed population using local range and dune country in the vicinity of the Cleland Hills. Within unit 2a, there is a band of large implements at c. 12,000–13,000 B.P. (95–98 cm below datum). The lithic assemblage from this part of unit 2a is larger and comparatively richer than that in earlier levels, the first pits or hearths appear, and these levels include the earliest grindstones. Camps were larger, as occupation debris now extended across most parts of the rock shelter floor, but must still have been of short duration as there was no attempt to clear large debris from occupation surfaces and other heavily trafficked areas.

Residential mobility remained high, but site territory (or site catchment) may been more limited. Excavated ochres show greater use of local sources and of ochre from Ulpunyali, the closest of the major ochre quarries to Puritjarra (50 km south east of the rock shelter). An earlier study of the ochres (Smith *et al.*, 1998) used a preliminary age estimate of 13,000 B.P. for the base of unit 2a. The revised chronology used here makes little difference to the conclusions of that study: Table 20 provides a breakdown of ochres by source within unit 2a, showing that the major changes in ochre provenance date to c. 12,000–13,000 B.P. rather than the base of 2a. The concentration of ochre near the rock shelter wall, suggests production of rock paintings from 13,000 B.P., though none of this pigment art survives today. Pecked engravings on boulders embedded in the floor of the shelter probably also date from this time period. Both paintings and engravings may signal a concern to more visibly assert rights and relationships to the site.

Table 20. Distribution of ochre in unit 2a. Data are number of pieces in each category.

analytical unit	depth below datum	group 1 (Karrku)	group 2 (Ulpunyali)	other ochres
2a	85–90 cm	—	—	—
2a	90–98 cm*	19 (36%)	12 (23%)	22 (41%)
2a	98–105 cm	6 (60%)	—	4 (40%)

* Levels dating between 10,500 B.P. and 12,000–13,000 B.P.

The mid Holocene (unit 1c)

After c. 7,500 B.P. people began to use the rock shelter more intensively, coinciding with the onset of conditions sufficiently humid to alter patterns of sedimentation and weathering in the rock shelter. There is a significant increase in artefact discard rates, more broken tools and broken cores, and both implements and cores are more heavily worked. Larger debris was cleared from the floor of the rock shelter, reflecting extended episodes of occupation. Grindstones become more common indicating greater use of plant processing gear. There was more use of locally available ochres and a greater reliance on local sandstone for artefacts. Except for white chalcedony, the use of non-local stone sources declines or remains low. Exotic silcrete virtually disappears from the sequence.

All this points to more local provisioning and visits to the rock shelter that on average were more sustained, not simply more frequent—and site territories that remained as restricted in extent as those at the time unit 2a accumulated. In many respects, unit 1c occupation continues trends in site use initiated around 13,000 B.P. in unit 2a.

Late Holocene occupation (units 1a–b)

From 3,500 B.P., the people visiting Puritjarra were using a more diverse tool kit, including hafted adzes and scrapers and other composite artefacts of wood, resin and stone—as well as specialized seed grinding implements for processing grass and acacia seeds. Unit 1b records increasing use of the rock shelter, with relatively high levels of breakage of cores and tools, of treadage and trampling, and of artefact reduction. The large increase in exotic stone and ochre in 1b signals a significant broadening of site catchment, reflecting either a shift in the way these materials were acquired (i.e. a shift to logistical procurement; or stronger social exchange networks), or a more complex mix of extended and short-term occupation during the accumulation of this unit.

There was a further substantial increase in use of the rock shelter around 800 B.P. (unit 1a). This involved a large increase in artefact discard rates, more pits and fireplaces, more ochre (especially from the Karrku mine), more grindstones (especially seed grinding implements which are more numerous in 1a than any other level) and the richest and most diverse tool inventory recorded at this site. By 800 B.P. Puritjarra was a core residential site with extended periods of occupation, and probably one of a number of such sites in the Cleland Hills. This shift may be underpinned by changes in regional environments as phytolith records at Puritjarra show that, during the last 1000–1500 years, grass levels stabilized at their highest values since the last interglacial, indicating greatly improved summer rainfall. Continuing the trend begun in unit 1b, occupation during the last 800 years may also have involved a dual pattern, with a marked seasonal component, frequent shorter visits, and frequent cycling of people through the site—intercalated with a pattern of extended episodes of occupation.

Implications

The Puritjarra sequence has implications for ideas about prehistoric land use in the Australian desert, though comparable data from other excavated sites is urgently required to establish the variability and extent of internal differentiation in these systems.

The nature of late Pleistocene occupation. Detailed analysis of the Puritjarra assemblages supports the notion that late Pleistocene groups in the Australian desert were small, highly mobile groups using large territories. In many respects, the archaeological pattern between 32,000–18,000 B.P. resembles an extreme form of the ethnographic pattern in the Western Desert: small groups, low population density, high residential mobility, and generalized foraging (i.e. residential mobility was high throughout the period of occupation at Puritjarra, but was more extreme in this earlier period). However, Puritjarra also shows there was considerable variability in late Pleistocene site patterns and assemblages, particularly between pre- and postglacial occupations. The postglacial levels of Puritjarra show evidence for larger, more geographically circumscribed groups using the rock shelter in the terminal Pleistocene and early Holocene, especially around 12,000–13,000 B.P.

Impact of the last glacial maximum. Puritjarra registers the impact of the heightened aridity around 18,000–20,000 B.P. on residential mobility and site territory, with an apparent shift to a pattern of more focussed or "water-tethered" occupation during the LGM. Populations appear to have persisted in western central Australia throughout this period (see similar evidence from Yirra rock shelter in the Pilbara, Veitch *et al.*, 2005). Continuities in tool inventories, stone technology, and in the sources of stone or red ochre reaching Puritjarra, suggest that any disruption to use of the rock shelter is more likely to reflect inter-decadal variability in regional environments than regional abandonment.

System response to environmental change. The pattern of phase shifts in occupation at Puritjarra suggests that models of *metastable equilibrium* have a role in understanding changes in land use in the arid zone. Metastable equilibrium is "where a specific catalyst or trigger carries a system over a threshold into a new equilibrium state" (Frankel, 1988: 41). The Puritjarra sequence suggests that sharp environmental transitions, such as those at 18,000 B.P. and 7,500 B.P., destabilized local patterns of land use and led to a re-positioning of cultural activities in the landscape. The new pattern was comparatively stable despite ongoing changes in regional environments, at least until the next major environmental spike. A similar response may help explain why the Western Desert site of Serpent's Glen, apparently abandoned around 24,000 B.P. as aridity increased, remained unoccupied until the mid Holocene at 4,700 B.P.

Late Holocene shifts in mobility patterns. At Puritjarra, evidence for a shift to a more mobile pattern of land use after 3,500 B.P. is equivocal at best. Any changes in group mobility in the late Holocene appear to have occurred within the context of more intensive occupation of the rock shelter. It is possible that a "home-range" pattern of seasonal or inter-annual movement would have increased the frequency of shorter visits to central places, such as Puritjarra, in between episodes of more extended use. However, other mechanisms—such as changes towards direct provisioning of stone and ochre as use of the shelter intensified, or more effective social exchange networks as regional population increased—may also account for the observed pattern. At Puritjarra, the last millennium sharpened this "dual" pattern, combining more intensive use of the rock shelter with the discard of larger quantities of exotic stone and ochre.

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DEDICATION. In memory of Rhys Jones (1941–2001), friend, mentor and exponent of research into the world of Late Pleistocene Australia.

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Appendix 1—Definitions of attributes

Stone artefact attributes used in this study follow definitions in Andrefsky (1998), Cotterell & Kamminga (1987), Holdaway & Stern (2004) and Hiscock (1986: 48–49). All metrical attributes were measured to the nearest mm.

Weight. Mass, measured to the nearest 0.1g but rounded to the nearest gram.

Length. For flakes, length is the maximum dimension parallel to the percussion axis (Andrefsky, 1998: fig. 5.8c). Where the percussion axis could not be determined, length was the maximum dimension of the artefact. For geometric microliths, where orientation of the artefact relative to the worked margin is important, it is the length of the edge opposite the backed margin.

Retouch length. Length of the longest contiguous section of retouch on an artefact.

Core height. Core height is the maximum dimension of a core taken at 90° to the major platform. Effectively it is core length. For discoidal or bifacial cores it is maximum thickness measured at 90° to the plane of the edge used as a striking platform and which bisects the core. For amorphous cores—which by definition cannot be oriented with respect to a striking platform—core height was taken to be the maximum linear dimension.

Breadth. For flakes, breadth is the distance between lateral margins measured at 90° to the percussion axis, midway along the length of the artefact (Andrefsky, 1998: fig. 5.9b). Where the percussion axis could not be determined, breadth was the maximum dimension of the artefact at 90° to the length, taken midway along the length of the artefact. For geometric microliths and tula adze flakes or slugs, breadth was the maximum dimension of the artefact at 90° to the length.

Thickness. Maximum distance through the artefact measured at 90° to breadth, midway along the length of the artefact (Andrefsky, 1998: fig. 5.9g). For geometric microliths, thickness was measured as the height of the backed margin.

Platform breadth. Distance across the platform between lateral margins (Andrefsky, 1998: fig. 5.5).

Platform thickness. Maximum distance across the platform (parallel to the surface) measured at 90° to platform breadth, without necessarily bisecting the ring-crack.

Platform angle. Exterior platform angle between the dorsal surface of a flake—or the face of a core—and the platform, measured to the nearest 5°.

Platform surface. Categorized as facetted (created by a series of small contiguous or overlapping flake scars); having several flake scars (created by >1 flake removals); having a single major flake scar; or cortical (all platforms which retain some cortex).

Edge angle. For flakes, edge angle is the spine-plane angle along the retouched edge to the nearest 5°. For block implements, it is the angle between major faces, along the retouched edge. This study did not routinely measure the retouch angle (producer angle) for several reasons: (*a*) the profile of the unmodified edge gives a better indication of the original steepness of an edge prior to use or modification, (*b*) this study looked at blank selection rather than discard state, and (*c*) most retouch on the Puritjarra artefacts could be considered to be either resharpening of an edge or use-damage.

Termination. The categories of flake termination used here (feather, hinge, step and plunging) follow Cotterell & Kamminga (1987).

Flake types. For flakes, three major fracture types are recognized (conchoidal, bending and bipolar) (Cotterell & Kamminga, 1987).

Cortex. This is a percentage of total surface area with cortex, recorded as an ordinal variable: no cortex; <5% cortex remaining; <50% cortex remaining; >50% cortex remaining. For flakes only the dorsal surface is included.

Flare. Parallel index for flakes (Hiscock, 1986), calculated by dividing the breadth by platform breadth. Values <1.0 indicate a flake with converging margins. Values >1.0 indicate a flake with flaring margins.

Notch width. This is maximum chord length of a notch.

Notch depth. This is the maximum depth of a notch, measured at 90° to notch width.

Appendix 2—Data sets

Several FileMaker Pro databases were created to facilitate analysis of the excavated artefacts. These are available on request from the author.

PJ/Spit Data. Basic data on the contents of each of the 336 excavation units or spits, with the depth of each excavation unit, the total weight of material excavated, the weight of each sieve fraction (6 mm and 3 mm) and of any rocks, and a breakdown of the sieve fractions by type of material (lithics, grindstones, ochre, charcoal, sandstone rubble). Counts or weights are given for each category as appropriate.

PJ/Lithics/Database-A/attribute data. Attribute data for 2622 individual artefacts. Attribute data is given for all cores (N = 131) and retouched artefacts (N = 687), and a sample of 931 unretouched flakes. All artefacts from layer II, including debitage, are entered in this database.

PJ/Lithics/Database-B/frequency data. Basic data for the entire excavated assemblage, which includes the number and weight of cores, flakes, retouched artefacts and debitage within each excavation unit. This is further broken down by raw material. This data file allows exploration of broad trends in artefact size or frequency, controlling variously for time period, raw material or artefact class using the entire assemblage.

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Systematic Position of *Trichadenotecnum enderleini* (Roesler) (Psocodea: "Psocoptera": Psocidae)

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ABSTRACT. *Trichadenotecnum enderleini* (Roesler, 1943) is the only native species of the genus known from Australia to date. However, its exact systematic position is not firmly fixed mainly due to the lack of information on taxonomically and phylogenetically important morphological characters. In this study, *T. enderleini* is examined morphologically to clarify further its systematic position. The forewing markings and male terminal structures clearly show that the species lacks all apomorphies of *Trichadenotecnum* Enderlein, 1909 and is thus only distantly related to the genus. Therefore, *T. enderleini* is excluded from *Trichadenotecnum*. *Ptycta floresensis* Endang, Thornton & New, 2002 from Indonesia is considered to be the closest relative of *T. enderleini*, and *T. enderleini* is consequently transferred to the genus *Ptycta* Enderlein, 1925. As a result, Australia is excluded from the distributional range of *Trichadenotecnum*, except for *T. circularoides* Badonnel, 1955 considered to be introduced.

YOSHIZAWA, KAZUNORI, & COURTENAY N. SMITHERS, 2006. Systematic position of *Trichadenotecnum enderleini* (Roesler) (Psocodea: "Psocoptera": Psocidae). *Records of the Australian Museum* 58(3): 411–415.

The genus *Trichadenotecnum* Enderlein, 1909 ("Psocoptera": Psocidae) has long been characterized by the superficial similarities of forewing markings and venation and has included a heterogeneous assemblage of species. Although recent morphological and molecular analyses provided a clear limit of the genus as a monophyletic group (Yoshizawa, 2001, 2003, 2004), further examination of some species placed currently in the genus is required to clarify their exact systematic position. In particular, the correct systematic placement of the only endemic Australian species of the genus, *T. enderleini* (Roesler, 1943) (Smithers, 1996), is needed to understand more clearly the distributional range and biogeography of the genus. Morphological characters of *T. enderleini* have not been examined since its original description, in which only fore- and hindwing venation and coloration were illustrated; no information on genital structures has been provided.

The species was originally described as *Psocus conspurcatus* Enderlein, 1903. Subsequently, the species was transferred to the genus *Trichadenotecnum* by Enderlein (1925) based on the superficial resemblance of forewing venation and markings. The specific epithet, *conspurcatus*, was preoccupied by *Psocus conspurcatus* Rambur, 1842 and thus Roesler (1943) gave the new specific epithet,

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enderleini, to the species and placed it in the genus *Psocidus s.l.* Thornton (1961) noted a possibility of close affinity between the species and the genus *Trichadenotecnum* based on the triangular areola postica and the spotted forewing. However, he did not make a formal nomenclatural statement concerning its generic placement. The species was transferred formally to the genus *Trichadenotecnum* by Smithers (1967), and this taxonomic treatment has been followed subsequently (see synonymy below).

The above taxonomic acts were done without detailed morphological information on the species. Especially, placement of the species in the genus *Trichadenotecnum* is based on superficial similarities of the forewing venation and markings. However, such venation and markings are known in some distantly related groups (Yoshizawa, 1998). Therefore, to decide the exact taxonomic position of the species, detailed information on important taxonomic and phylogenetic characters (e.g., male terminalia) is required. In the present paper, *Trichadenotecnum enderleini* is examined morphologically and its systematic position is discussed.

Methods of morphological examination follow Yoshizawa (2002). All specimens examined are in the Australian Museum, Sydney.

Systematics

Ptycta enderleini (Roesler) n.comb.

Figs 1–3

Psocus conspurcatus Enderlein, 1903: 224 (type locality: Royal Botanical Gardens Sydney, NSW, Australia).—Junior homonym of *Psocus conspurcatus* Rambur, 1842.

Trichadenotecnum conspurcatum (Enderlein).—Enderlein, 1925: 105.

Psocus enderleini Roesler, 1943: 13 (new name for *P. conspurcatus* Enderlein).

Psocidus enderleini (Roesler).—Roesler, 1943: 13; Thornton, 1961: 2.

Trichadenotecnum enderleini (Roesler).—Smithers, 1967: 115; Smithers, 1977: 290; Smithers, 1996: 75; Lienhard & Smithers, 2002: 464.

Material examined. AUSTRALIA, NEW SOUTH WALES: 1 ♀, Lake Cathie, nr Port Macquarie, 12.v.1977, A.S. & C.N. Smithers; 2 ♂ ♂ 1 ♀, Trial Bay Gaol, 12.v.1977, C.N. & A.S. Smithers; 3 ♂ ♂ 3 ♀ ♀, Golden Hole, 10 km S. Stuarts Pt, 13.v.1977, C.N. & A.S. Smithers; 2 ♂ ♂, Broadwater Nat. Park, 6.v.1978, C.N. Smithers; 1 ♂, Wyrrabalong Nat. Park, 27.xi.1997, L. Wilkie; 1 ♀, Bola Creek, Nat. Park, 6.x.1965, A.S. Smithers.

Redescription. *Male*. Head white in ground colour; vertical and orbital markings brown; coronal suture pale; epicranial suture bordered with narrow brown band dorsally; frons pale brown, with irregular brown spots; eye black, large, IO/D= 0.85; ocelli white, ocellar field blackish brown; gena white; antennal socket bordered with narrow brown band; postclypeus with c. 10 longitudinal rows of brown spots; anteclypeus pale brown. Antenna pale brown, scape and pedicel slightly darker. Mouth parts white, tip of fourth segment of maxillary palpus blackish brown. Thorax. Prothorax brown. Mesonotum brown except median part, anterior lobe and lateral margins of lateral lobes of scutum white; scutellum brown; postnotum blackish brown. Metanotum brown except anterior lobe of scutum white. Meso- and metapleura blackish brown except membranous regions white. Legs white; mid and hind coxae brown; all femora with blackish brown marking near distal end; 2nd tarsomere and claws brown. Forewing (Fig. 1) hyaline with brown markings; distal region sparsely covered with small spots; medially with narrow brown band running from posterior corner of pterostigma through centre of discoidal cell to distal end of cell cup; basal quarter with broad band widely interrupted around vein M. Pterostigma white except distal ⅖; posterior margin brown. Anal cell brown in basal half. Veins blackish brown except along Rs fork, distal half of M closing discoidal cell, and CuA_2 white; Rs fork acute; areola postica almost triangular. Hindwing hyaline; veins brown except R1, basal section of Rs and Rs+M paler. Abdomen white except first segment and terminalia brown. Terminalia (Fig. 2): Posteroventral region of clunium (Fig. 2A) widely membranous. Eighth sternum (Fig. 2A) without sclerite. Epiproct (Fig. 2B) with two pairs of long setae laterally; epiproct lobe weakly expanded dorsally. Paraproct (Fig. 2A) with large basal lobe dorsally and with cone-like projection posteromedial to trichobothrial field; distal process very long, strongly curved. Hypandrium (Fig. 2C) symmetrical, deeply incised at middle; posterodorsal arms bulbous, each with row of tiny denticles; posterodorsal region with two pairs of processes, external pair small, triangular, arising just below bulbous arms, internal pair large, each with broad and rounded base and pointed distal end; lateral region covered with denticles; median region with longitudinal row of long and transparent articulated spines just below incision; ventral region with two pairs of processes, external pair small, internal pair long. Phallosome (Fig. 2D,E) very long; phallobase with well-developed lateral process, anteroventrally rounded. Length (mm): body (B) 2.5–3.0; forewing (FW) 3.4–3.7; hindwing (HW) 2.6–2.9.

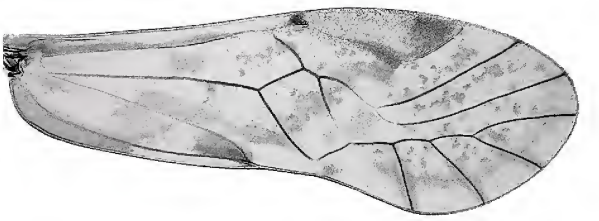

Fig. 1. Forewing of *Ptycta enderleini*, male.

Female. Coloration and general morphology, except terminalia, almost as in male; pigmentation much paler, probably due to long alcohol preservation; eye small, IO/D= 2.0. Genitalia (Fig. 3): Egg guide of subgenital plate (Fig. 3A) almost as long as wide, parallel sided, apical margin almost straight, with six thick setae and many fine setae, lateral margin also with few strong setae; body of subgenital plate V-shaped but very slightly pigmented, probably due to long alcohol preservation. Ventral valve of gonapophyses (Fig. 3B) short; dorsal valve narrow; external valve without posterior lobe, anteroexternally with thumb-shaped lobe. Internal plate well sclerotized. Length: B 2.8–3.2; FW 3.8–4.0; HW 2.7–3.0.

Distribution. Australia (NSW).

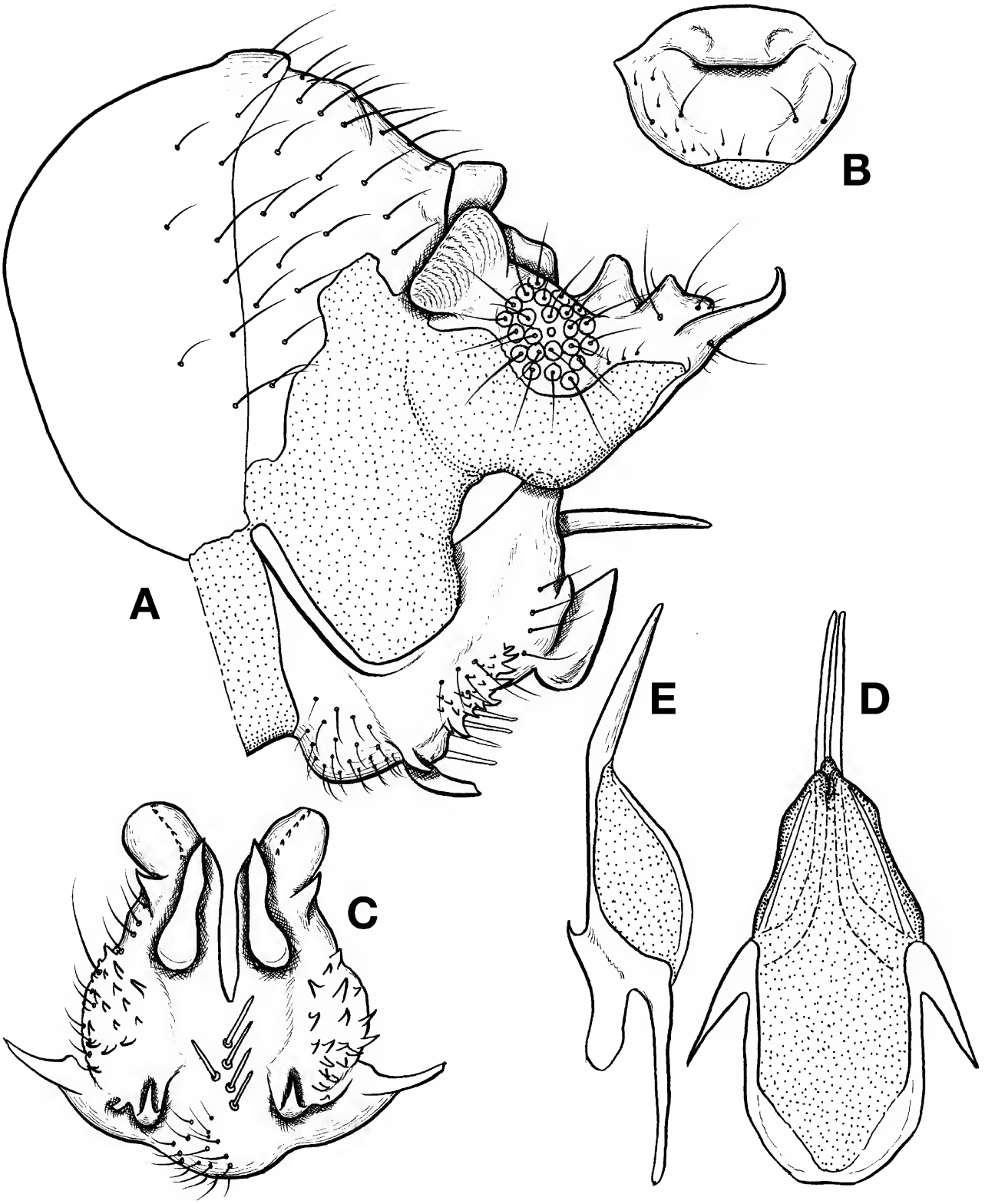

Fig. 2. Male terminal structures of *Ptycta enderleini*. (*A*) Terminalia, lateral view. (*B*) Epiproct, dorsal view. (*C*) Hypandrium, posterior view. (*D*) Phallosome, ventral view. (*E*) Ditto, lateral view.

Remarks. *Ptycta enderleini* is most similar to *P. floresensis* Endang, Thornton & New, 2002 in forewing markings (especially in the female), medially incised hypandrium, and apically elongated phallosome. In particular, the apically elongated phallosome is apomorphic and uniquely shared by *P. floresensis* and *P. enderleini*; this character state indicates their close affinity. Female structures of gonapophyses in *P. enderleini*, such as the narrow dorsal valve and lack of the posterior lobe of the external valve, are similar to *P. verticalis* Vaughan, Thornton & New, 1991 and *P. merapiensis* Endang, Thornton & New, 2002. However, *P. enderleini* can be easily distinguished from these species by the unique forewing markings and the hypandrial structures.

Discussion

We conclude that *P. enderleini* cannot be assigned to the genus *Trichadenotecnum* because of lack of all apomorphies supporting the monophyly of the genus (Yoshizawa, 2001, 2003). For example, the forewing of *P. enderleini* lacks the six submarginal spots and opposing spots in cell r which characterize the genus *Trichadenotecnum*. Rather, presence of the paraproctal basal lobe in the male suggests that the species is related to the genus *Copostigma* Enderlein, 1903 (Smithers, 1985; Endang *et al.*, 2002).

However, *P. enderleini* lacks an important apomorphic character of *Copostigma*, namely a cross vein connecting Rs and M in the forewing. In addition, the male genital structures in Psocidae are known to be highly variable and sometimes homoplasious (e.g., Yoshizawa, 2004; Yoshizawa & Lienhard, 2004), and the paraproctal basal lobe observed in *Copostigma* and *P. enderleini* might also possibly have evolved independently; this should be tested on the basis of molecular phylogeny. Here, we place this species in the genus *Ptycta* Enderlein, 1925, following the treatment by Endang *et al.* (2002). Judging from the morphological features, the closest relative of *P. enderleini* is considered to be *P. floresensis* Endang, Thornton & New, 2002 (see remarks above). In addition, some species of *Ptycta* are known to possess the paraproctal basal lobe in males (e.g., Endang *et al.*, 2002). Therefore, placement of *P. enderleini* under the genus *Ptycta* is considered to be the best solution at present. However, as mentioned by Lienhard & Smithers (2002) and Endang *et al.* (2002), the genus *Ptycta* now includes many heterogeneous species and is thus possibly

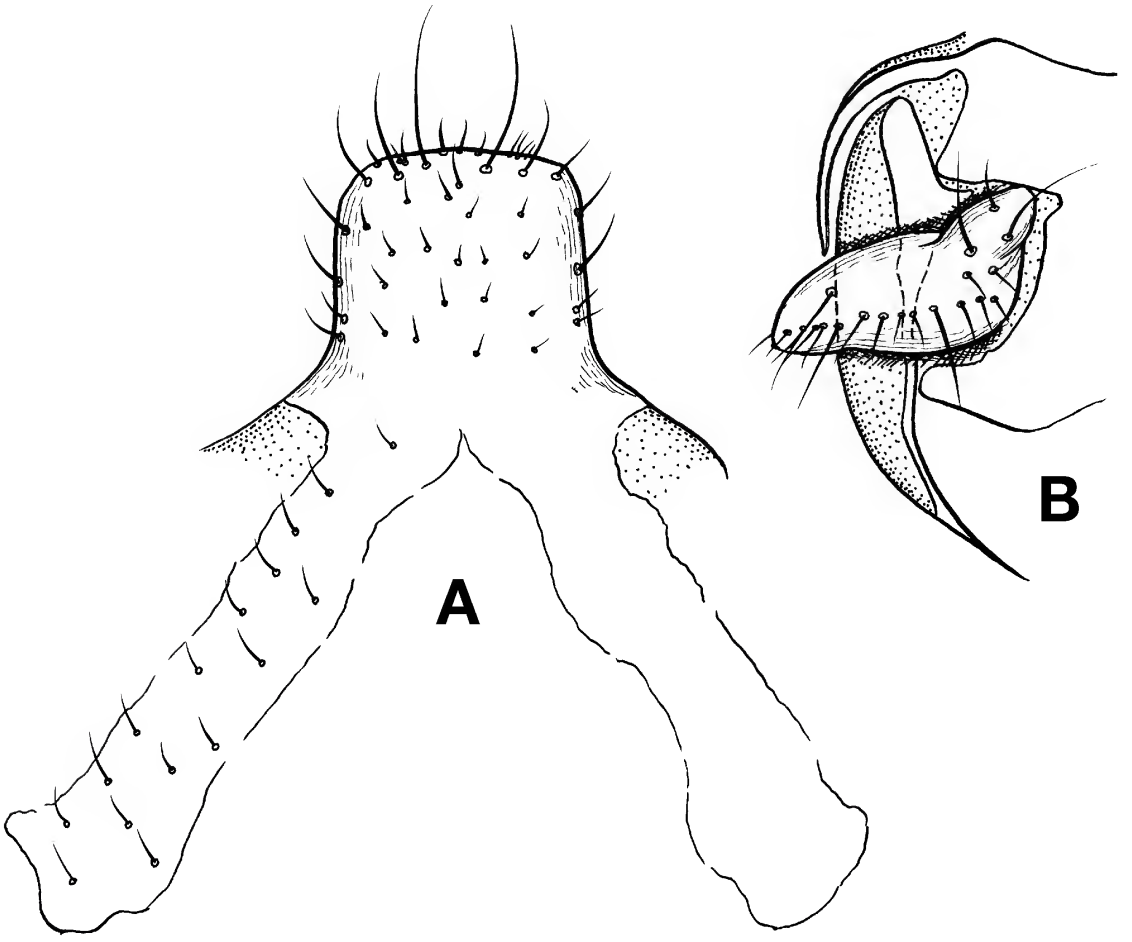

Fig. 3. Female genitalia of *Ptycta enderleini*. (*A*) Subgenital plate, ventral view, setae on right half omitted. (*B*) Gonapophyses, ventral view.

polyphyletic. Therefore, its generic status and the higher systematics of the genus complex *Clematostigma-Copostigma-Mecampsis-Ptycta* must be revised by detailed morphological and molecular analyses based on a wide range of taxon sampling (Smithers, 1983; Lienhard & Smithers, 2002; Endang *et al.*, 2002).

Australia is thus excluded from the distributional range of the genus *Trichadenotecnum* except for *T. circularoides* Badonnel, 1955 which was recorded from Queensland, Australia by Yoshizawa (2004). For the following reasons, it is considered that the species is probably introduced to Australia and is not native: (*a*) the species shows extremely broad distributional range (Mockford, 1993; Yoshizawa, 2001; Lienhard & Smithers, 2002); (*b*) Australian and Japanese populations of *T. circularoides* show completely identical gene sequences (cytochrome oxidase I, NADH dehydrogenase subunit 5, 12S, 16S and 18S rDNA: Yoshizawa, unpublished data; those sequences of the Australian sample are available online at GenBank); (*c*) close relatives of the species are known only from Central and South America (Mockford, 1993; Yoshizawa, unpublished data).

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Caprellidae (Crustacea: Amphipoda) from the Great Barrier Reef and Adjacent Localities

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ABSTRACT. The caprellid fauna of the Great Barrier Reef region is investigated. The study reports 22 species in 17 genera. Three new genera and seven new species are described (*Hircella berentsae* n.sp., *Jigurru vailhoggett* n.gen., n.sp., *Mayericaprella arimotoi* n.gen., n.sp., *Orthoprotella pearce* n.sp., *Perotripus keablei* n.sp., *Pseudoprellicana johnsoni* n.gen., n.sp. and *Quadrisegmentum lowryi* n.sp.). All species are figured and a key to the species is provided. An ecological study conducted at Lizard Island, northern Great Barrier Reef, showed that *Metaprotella sandalensis* Mayer, 1898 and *Quadrisegmentum triangulum* Hirayama, 1988, were the most common species in the coral reef system. Although the caprellids were present at most sites around the Island, they were abundant only on hydroid and sediment substrates.

GUERRA-GARCÍA, JOSÉ M., 2006. Caprellidae (Crustacea: Amphipoda) from the Great Barrier Reef and adjacent localities. *Records of the Australian Museum* 58(3): 417–458.

Caprellid amphipods are small peracaridan crustaceans important as secondary and tertiary producers in marine ecosystems. They are common on algae, hydroids, bryozoans, sponges and seagrasses (McCain, 1968), and are important prey for many coastal fish species (Caine, 1987, 1989, 1991). Recently, caprellids have been found to be useful bioindicators of marine pollution and environmental stress (Guerra-García & García-Gómez, 2001; Takeuchi *et al.*, 2001) adding impetus to understand the taxonomy and systematics of this group of crustaceans.

The Caprellidae of the Great Barrier Reef have not been previously studied. The scarce work existing on the Amphipoda of this area has focused on the Gammaridea; K.H. Barnard (1931) reported 14 species of gammaridean amphipods collected by the 1928–1929 Great Barrier Reef Expedition, and Berents (1983) conducted the first study of the melitid gammarideans from tropical Australia. McCain & Steinberg (1970) listed 27 caprellid species from Australian waters, 14 in New South Wales, seven in Western Australia, three in Victoria and nine in Tasmania, but none from Queensland. Apart from the revision of McCain & Steinberg (1970), no taxonomic studies on the Caprellidae have been conducted along the Great Barrier Reef, and the only recorded species are those listed in ecological papers on benthic communities. In a list of the Crustacean species inhabiting the soft bottoms communities from Lizard Island, Queensland, Jones (1984) reported two caprellid species: *Metaprotella* sp. and *Phtisica marina* Slabber, 1769. Jones' (1984) specimens, deposited in the collections of the Australian Museum, are referable to *Metaprotella sandalensis* Mayer, 1898 and *Metaproto novaehollandiae* (Haswell, 1880) respectively.

The present study reports on the Caprellidae of the Great Barrier Reef and adjacent localities based primarily on museum collections. Additionally, a field study was conducted at Lizard Island in October 2001 to collect abundant material and to study habitat use by caprellids in a coral reef system.

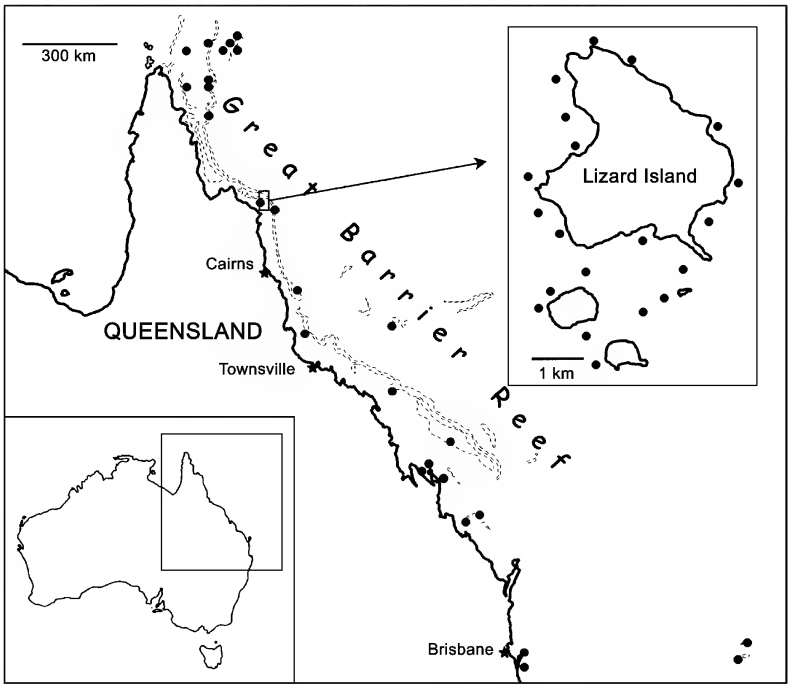


Fig. 1. Map of the study area showing the localities where samples were collected (●), and the location of Lizard Island in the Great Barrier Reef.

Material and methods

Material examined. Abundant caprellid material from the Great Barrier Reef and adjacent localities was comprehensively studied in the present work. Most specimens were collected by part of several Australian Museum surveys in the area. Smaller collections from the Queensland Museum are also included. When necessary, type material was consulted and studied. Measurements of specimens are in millimetres (mm) and setal formulae for mouthparts follow Laubitz (1993). Specimens are deposited in the following institutions:

AM	Australian Museum, Sydney
QM	Queensland Museum, Brisbane
USNM	National Museum of Natural History, Smithsonian Institution, Washington D.C.
ZMA	Zoologisch Museum, Amsterdam
ZMUC	Zoological Museum, University of Copenhagen, Copenhagen

Study area. Most of the samples were collected from the Great Barrier Reef (Fig. 1) This is the largest coral reef system in the world, extending 2000 km along the Queensland coast. It supports one of the most diverse ecosystems known, including a rich diversity of coastal habitats, coral reefs and cays, and continental islands. In addition to the samples from the Great Barrier Reef, collections from other areas of Queensland and the Tasman Sea, such as Shoalwater Bay, the coast near Brisbane, Middleton and Elizabeth Reefs, and Lord Howe Island, were studied in the present work. On the coast around Shoalwater Bay different habitats, as mangroves and seagrass beds, were sampled; most of this sampling area were characterized by wide tidal range, strong currents, not clear waters, and silty reefs. The fringing coral reef at Lord Howe Island is the southernmost in the world and the reefs at Elizabeth and Middleton Reefs represent the southernmost coral atolls. Elizabeth and Middleton Reefs are located about 725 km south of the southern end of the Great Barrier Reef and 95 km north of Lord Howe Island. Although coral species are fewer than on tropical reefs, the coral in these areas show few signs of human impact. Further details regarding Lord Howe Island, Middleton and Elizabeth Reefs can be found in Recher & Ponder (1981) and Whitley (1937), respectively.

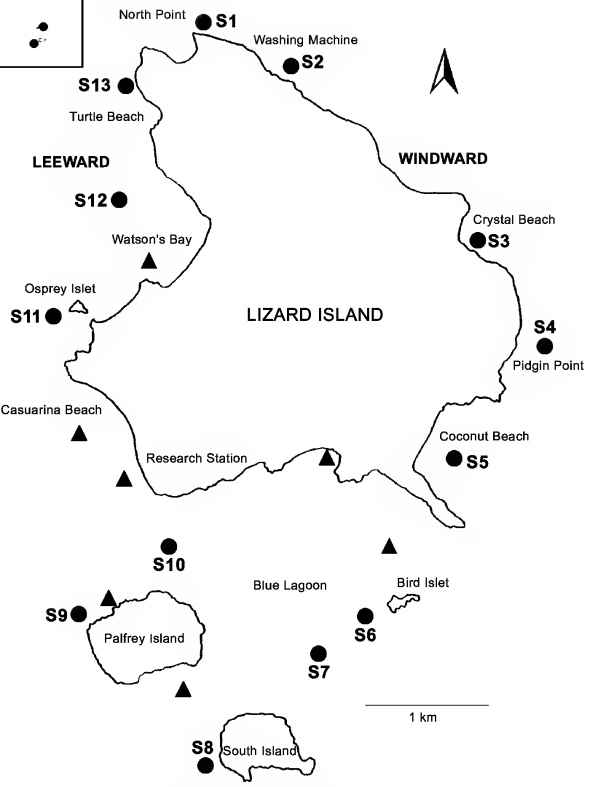


Fig. 2. Map of Lizard Island showing the sampling sites. Circles (●) indicate the localities sampled on SCUBA (numbered S1 to S13 for multivariate analysis) and the triangles (▲) the stations sampled on snorkel.

Lizard Island. Lizard Island (14°40'S 145°28'E) is a tropical, granitic, continental island c. 7 km^2 in area, located in the northern region of the Great Barrier Reef (Fig. 1). It is almost entirely fringed by coral reefs, which extend to

encompass two nearby islands (South and Palfrey) and a 10–12 m deep lagoon (Blue Lagoon) (Fig. 2). Lizard Island supports a diverse range of habitats: reef flats and slopes, algae and seagrass beds, coral rubble, fine and coarse sediments, and mangroves. A more detailed description of the island is given in Keable (1995), and a characterization of the sediments is given in Fisk (1983) and Jones (1984).

General collections along the Great Barrier Reef and adjacent localities. Most of the Great Barrier Reef material studied here was collected by the Australian Museum (see Station List in the Appendix). The purpose of these samplings was to collect small marine invertebrates, like amphipods and another peracarid crustaceans. Intertidal samples were collected by hand at low tide. Sublittoral samples were taken on SCUBA. Collecting techniques varied according to habitat. The majority of the samples were collected by hand, using fine nylon mesh bags or plastic bags. Occasionally, an air-lift was used to sample sediments and the epifauna of coral heads and gorgonians. Some samples of reef rock and dead coral were taken using a hammer and chisel. Samples were fixed in 7% neutralized formalin, and transferred to 70% ethanol.

Field study at Lizard Island. A sampling programme targeting caprellids was conducted at Lizard Island in October 2001. Twenty sites were sampled around the island, thirteen on SCUBA, and seven on snorkel (Fig. 2). These covered a wide diversity of habitats from the intertidal to 27.5 m deep. At each station, along a decreasing deep transect, the different habitats were explored and about 200 samples of potential substrates for the Caprellidae were collected (Table 1), including algae (20 species), seagrasses (3 species), sponges (18 species), hydroids (9 species), gorgonians (5 species), soft corals (4 species), bryozoans (3 species), ascidians (4 species), encrusted dead corals, coral rubble, fine and coarse sediments and mangroves. Although the echinoderms and most of the hard corals were not directly sampled, they were checked for caprellids "in situ". The most abundant algae were *Halimeda micronesica, H. macroloba, H. cilindracea, Padina* cf. *gymnospora, Galaxaura marginata* and *Turbinaria ornata*. The seagrasses were dominated by *Halophila* spp., which alternate with the algae, *Caulerpa* spp. Among the sponges were common *Spirastrella vagabunda* and *Pericharax heteroraphis*. The most common hydroids were *Macrorhynchia philippina* and *Aglaophenia cupressina*. The gorgonians *Junceella* spp. and *Mopsella* spp., and the soft coral *Nephtea* spp. were common at some sites. The bryozoans were seldom encountered, although *Heteroprellina denticulata* was present at several localities. The tunicate *Polycarpa aurata* was widely distributed along the whole island. Fine to coarse shelly sediments were sampled, on some occasions containing great amounts of the large foraminifera *Marginopora vertebralis*. Mangrove habitats, dominated by *Rizophora* sp., were also sampled.

The soft bottom samples were collected by hand, using fine nylon mesh bags that were dragged five to ten meters along the bottom. Other samples were placed in fine mesh or plastic bags. To avoid damage to specimens caused by

Table 1. Species composition of the Caprellidae collected from Lizard Island, Queensland, Australia. The qualitative values of abundance of caprellids in the different habitats are included. Qualitative scale: ○ absent; • rare (1–10 individuals/sample); ••, common (10–100 ind/sample); •••, very common (>100 ind/sample). All the data included in the table were collected during the sampling programme at Lizard Island in October 2001 except for *Pseudoprellicana johnsoni* (not found in October 2001, and the data are taken from previous surveys at Lizard Island) and *Quadrisegmentum lowryi* (data combined, collected from sponges in October 2001 but on coral rubble in previous surveys).

	algae	seagrass	sponges	hydroids	gorgonians	soft corals	dead hard corals encrusted	bryozoans	ascidians	coral rubble	coarse shelly sediment	fine sediment	mangroves
number of samples	45	12	25	25	12	4	17	4	7	13	14	10	4
Aciconula australiensis Guerra-García, 2004	○	○	○	•	○	○	•	○	○	○	○	○	○
Hemiaegina minuta Mayer, 1890	○	○	○	•	○	○	○	○	○	○	○	○	○
Jigurru vailhoggett n.gen., n.sp.	○	○	○	○	○	○	•	○	○	○	○	○	○
Metaprotella sandalensis Mayer, 1898	•	•	•	••	•	•	•	•	•	•	•	•	•
Metaproto novaehollandiae (Haswell, 1880)	○	○	○	○	○	○	○	○	○	○	•••	•••	○
Orthoprotella australis (Haswell, 1880)	○	○	○	•••	○	○	○	○	•	○	○	○	○
Orthoprotella mayeri Barnard, 1916	○	○	○	•	○	○	○	○	○	○	○	○	○
Orthoprotella pearce n.sp.	○	○	○	••	○	○	○	○	○	○	○	○	○
Perotripus keablei n.sp.	○	○	○	○	○	○	○	○	○	○	•	•	○
Protella similis Mayer, 1903	○	○	•	•••	○	○	○	○	○	○	•	○	○
Protogeton inflatus Mayer, 1903	○	○	○	○	○	○	○	○	○	○	○	•	○
Pseudaeginella biscaynensis (McCain, 1968)	○	○	○	•	○	○	○	○	○	○	○	○	○
Pseudoprellicana johnsoni n.gen., n.sp.	○	○	○	○	○	○	○	○	○	○	•	○	○
Pseudoproto fallax Mayer, 1903	○	○	○	○	○	○	•	○	○	○	○	○	○
Quadrisegmentum lowryi n.sp.	○	○	•	○	○	○	○	○	○	•	○	○	○
Quadrisegmentum triangulum Hirayama, 1988	•	•	•	○	••	○	•	○	•	•	○	○	○

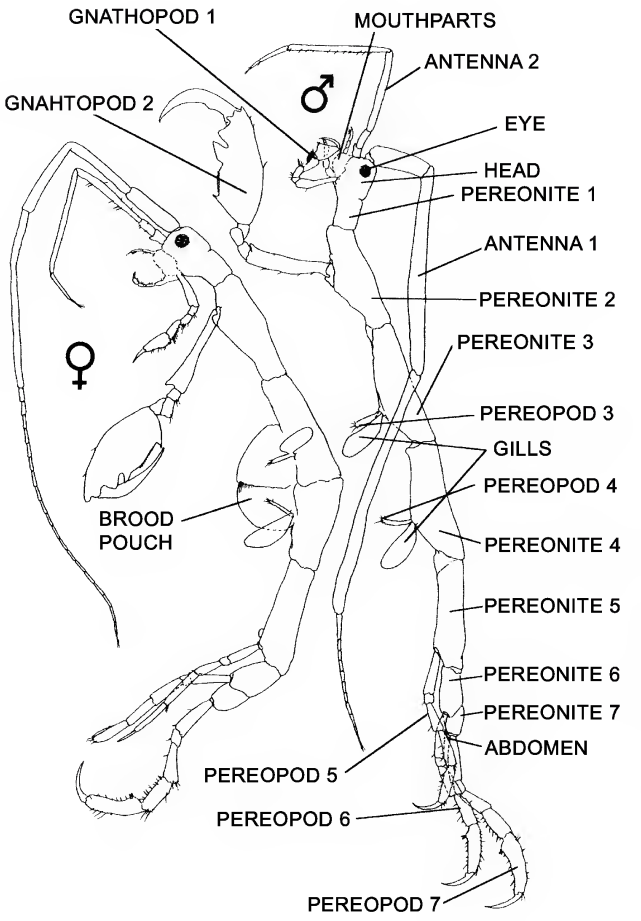


Fig. 3. Lateral view of a generalized caprellid.

sieving the sediment, caprellids were separated from sediment by eluting, forcing water through the sediment and allowing the small crustaceans to float to the surface. All samples were fixed in 95% ethanol.

The abundance of caprellids on different substrates was characterized using a qualitative scale: rare (1–10 individuals/sample), common (10–100 ind./sample) and very common (>100 ind./sample). Similarities among caprellid species based on ecological preferences were established by classification analysis. A similarity matrix for the classification was derived using the Bray-Curtis index (Bray & Curtis, 1957). This index was chosen because it does not consider double absences. The UPGMA aggregation algorithm was used (Sneath & Sokal, 1973). Similar classification analysis has been successfully used in other ecological studies working with qualitative scales as in the present study (Carballo *et al.*, 1996; Guerra-García, 2001).

Trade winds influence the physical conditions around the island. These blow consistently between 15 and 20 knots from the southeast between mid-March and September each year (Keable, 1995). Therefore, the island has been traditionally considered to have leeward sites on the west coast and windward sites on the east coast. To determine if the composition of the Caprellidae community differed between sides of the island, the 13 stations sampled on SCUBA were selected for the analysis. Although the sampling of the Caprellidae was qualitative, approximately the same collecting effort (in time and number of samples) was made in all stations. Therefore, a matrix of presence/absence of the caprellid species at each station was constructed. The affinities among stations on the basis of the caprellid community were established through cluster analysis using the UPGMA method and the Bray Curtis similarity index. To confirm the results of the cluster, an MDS analysis (non-metric multidimensional scaling) was used with the matrix. To test the ordination, the stress coefficient of Kruskal & Wish (1978) was employed. Multivariate analyses (classification and ordination) were carried out using the program PC-ORD v.305 (McCune & Mefford, 1997) and PRIMER package (Clarke & Gorley, 2001)

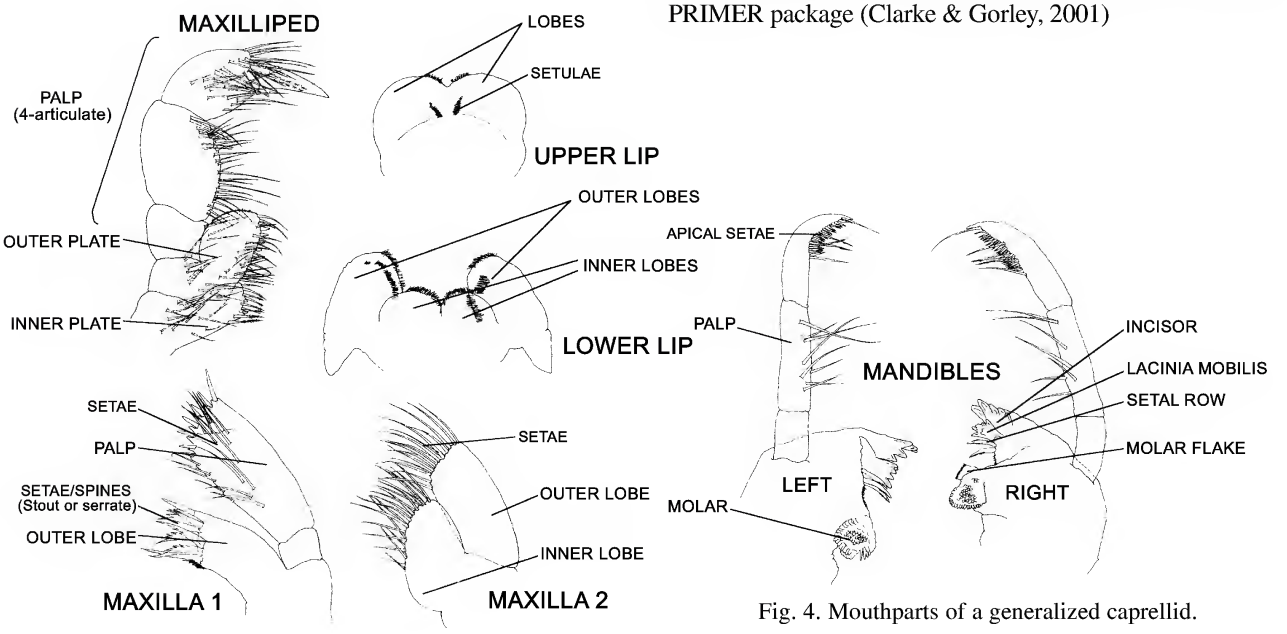


Fig. 4. Mouthparts of a generalized caprellid.

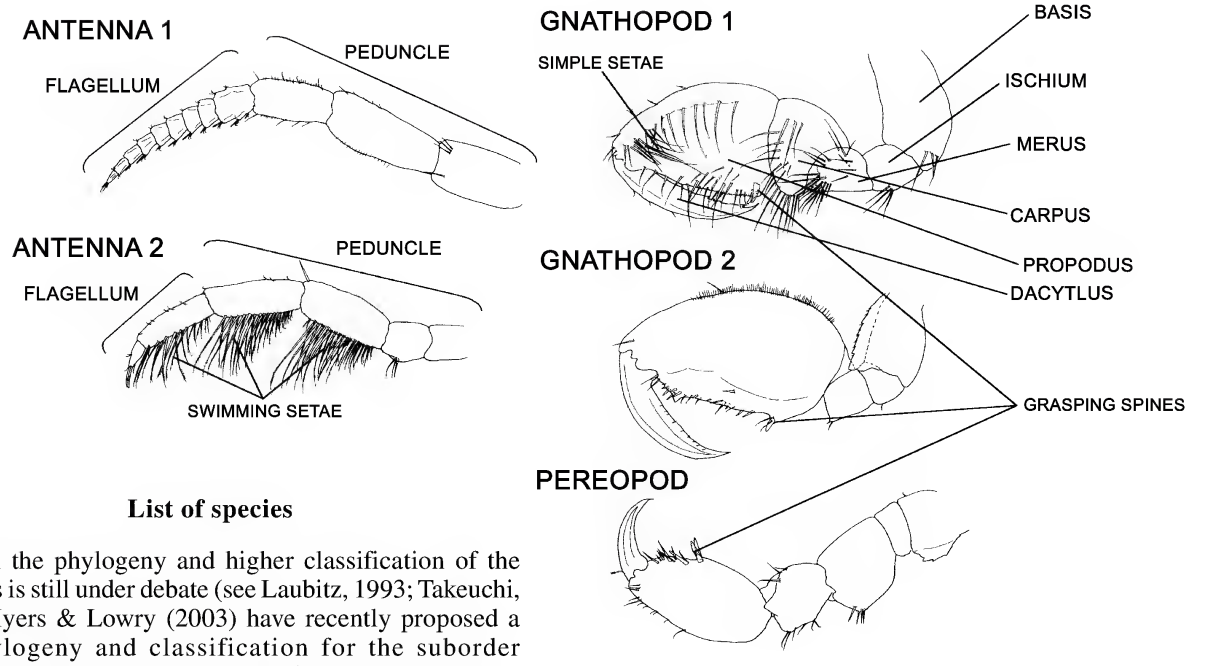


Fig. 5. Antennae, gnathopods and pereopod of a generalized caprellid.

List of species

Although the phylogeny and higher classification of the caprellids is still under debate (see Laubitz, 1993; Takeuchi, 1993), Myers & Lowry (2003) have recently proposed a new phylogeny and classification for the suborder Corophiidea Leach, 1814, comprising two infraorders, Corophiida and Caprellida, based on a hypothesis of the evolution of different feeding strategies. In their new classification, adopted here, the superfamily Caprelloidea includes five families: Caprellidae, Caprogammaridae, Cyamidae, Dulichiidae and Podoceridae. Caprellidae comprises three subfamilies: Caprellinae, Paracercopinae and Phtisicinae. The present study focuses on members of the Caprellidae. Figures 3–6 include drawings of a generalized caprellid showing the terminology used throughout the manuscript.

Infraorder Caprellida Leach, 1814
Superfamily Caprelloidea Leach, 1814
Family Caprellidae Leach, 1814

Subfamily Phtisicinae Vassilenko, 1968

Hircella berentsae n.sp. (Figs 7–11)
Hircella cornigera (Haswell, 1879) (Fig. 12)
Jigurru vailhoggett n.gen., n.sp. (Figs 13–17)
Mayericaprella arimotoi n.gen., n.sp. (Figs 18–22)
Metaproto novaehollandiae (Haswell, 1880) (Fig. 23)
Perotripus keablei n.sp. (Figs 24–27)
Protogeton inflatus Mayer, 1903 (Fig. 28)
Pseudoprellicana johnsoni n.gen., n.sp. (Figs 29–32)
Pseudoproto fallax Mayer, 1903 (Fig. 33)
Quadrisegmentum lowryi n.sp. (Figs 34–38)
Quadrisegmentum triangulum Hirayama, 1988 (Fig. 39)

Subfamily Caprellinae Leach, 1814

Aciconula australiensis Guerra-García, 2004 (Fig. 40)
Caprella danilevskii Czerniavskii, 1868 (Fig. 41)
Caprella penantis Leach, 1814 (Fig. 42)
Hemiaegina minuta Mayer, 1890 (Fig. 43)
Metaprotella sandalensis Mayer, 1898 (Fig. 44)
Orthoprotella australis (Haswell, 1880) (Fig. 45)
Orthoprotella mayeri Barnard, 1916 (Fig. 46)
Orthoprotella pearce n.sp. (Figs 47–51)
Paracaprella sp. (Fig. 52)
Protella similis Mayer, 1903 (Fig. 53)
Pseudaeginella biscaynensis McCain, 1968 (Fig. 54)

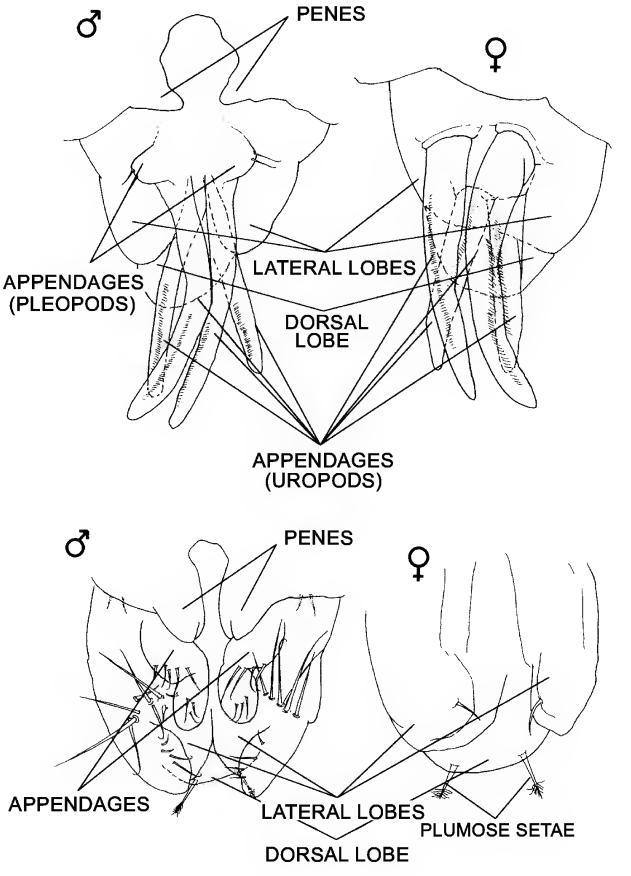


Fig. 6. Abdomen of generalized caprellids.

Key to the species of Caprellidae from the Great Barrier Reef and adjacent localities

This key can be used without dissection but should be used in conjunction with Figs 3–6

1 Gills present on pereonites 2, 3 and 4 2
—— Gills present on pereonites 3 and 4, absent on pereonite 2 10

2 Pereopods 3 and 4 six-articulate 3
—— Pereopods 3 and 4 absent or reduced to a tiny article 6

3 Pereopod 5 four-articulate 4
—— Pereopod 5 five-articulate 5

4 Antenna 1 clearly shorter than the body. Pereopods 3 and 4 shorter than pereonites 3 and 4 combined. Propodus of the male gnathopod 2 with a triangular projection ..... *Quadrisegmentum triangulum* (Fig. 39)
—— Antenna 1 as long as body. Pereopods 3 and 4 longer than pereonites 3 and 4 combined. Propodus of the male gnathopod 2 without triangular projection ..... *Quadrisegmentum lowryi* (Figs 34–38)

5 Abdomen with a pair of appendages ..... *Metaproto novaehollandiae* (Fig. 23)
—— Abdomen without appendages ..... *Pseudoproto fallax* (Figs 33)

6 Pereopod 5 absent or reduced to one tiny article 7
—— Pereopod 5 present, three to six-articulate 8

7 Body smooth, without acute dorsal projections ..... *Hircella berentsae* (Figs 7–11)
—— Body with acute dorsal projections ..... *Hircella cornigera* (Fig. 12)

8 Pereopods 3 and 4 reduced to one tiny article. Flagellum of antenna 1 2-articulate. Body geniculate ..... *Perotripus keablei* (Figs 24–27)
—— Pereopod 3 and 4 absent. Flagellum of antenna 1 more than 2-articulate. Body not geniculate 9

9 Pereonite 3 with a pair of well-developed projections ..... *Mayericaprella arimotoi* (Figs 18–22)
—— Pereonite 3 without projections ..... *Jigurru vailhoggett* (Figs 13–17)

10 Pereopods 3 and 4 six-articulate ..... *Protogeton inflatus* (Fig. 28)
—— Pereopods 3 and 4 absent or reduced to one or two articles 11

11 Pereopods 3 and 4 absent 12
—— Pereopods 3 and 4 reduced to one or two articles 14

12 Pereopod 5 3-articulate ..... *Pseudoprellicana johnsoni* (Figs 29–32)
—— Pereopod 5 six-articulate 13

13 Head with a well-developed rostrum ..... *Caprella penantis* (Fig. 42)
—— Head with a small rostrum ..... *Caprella danilevskii* (Fig. 41)

14 Pereonites 6 and 7 fused ..... *Metaprotella sandalensis* (Fig. 44)
—— Pereonites 6 and 7 not fused 15

15 Head and/or body with dorsal projections 16
—— Head and body completely smooth dorsally 18

16 Pereonite 4 2-articulate ..... *Aciconula australiensis* (Fig. 40)
—— Pereonite 4 one-articulate 17

17 Head with two acute projections. Body smooth ..... *Orthoprotella australis* (Fig. 45)
—— Head with a single acute projection. Body with numerous rounded projections ..... *Pseudaginella biscaynensis* (Fig. 54)

18 Pereopods 3 and 4 2-articulate 19
—— Pereopods 3 and 4 one-articulate 20

19 Pereopods 3 and 4 minute, shorter than half length of gills ..... *Paracaprella* sp. (Fig. 52)
—— Pereopods 3 and 4 longer than half length of gills ..... *Orthoprotella mayeri* (Fig. 46)

20 Suture between head and pereonite 1 absent. Pereonite 2 with acute ventral projection between gnathopod 2 ..... *Hemiaegina minuta* (Fig. 43)
—— Suture between head and pereonite 1 present. Pereonite 2 without acute ventral projection 21

21 Peduncle of antenna 1 distinctly longer than half body length ..... *Protella similis* (Fig. 53)
—— Peduncle of antenna 1 about ⅓ body length ..... *Orthoprotella pearce* (Figs 47–51)

Systematic account

Subfamily Phtisicinae Vassilenko, 1968

Hircella Mayer, 1882

Hircella berentsae n.sp.

Figs 7–11

Type material. HOLOTYPE ♂, AM P61610, outer slope, W of "Yoshin Maru Iwaki", Elizabeth Reef, Australia, 29°57.2'S 159°01.2'E, coral rubble, 8–24 m, St 30, J.K. Lowry & R.T. Springthorpe, 12 Dec 1987. PARATYPES: 1♀, AM P61611, type locality; 2♂♂, 3♀♀, AM P61612, type locality.

Additional material examined. 1 juvenile AM P61653 (QLD 980); 4♂♂, 2♀♀, 1 juvenile, AM P61613 (st 14); >20 specimens, AM P61614 (st 21); 3♀♀, AM P61615 (st 30); 2♀♀, AM P61616 (st 36); 2♀♀, AM P61617 (st 43).

Etymology. This species is named after Penny Berents, Australian Museum, for her kindness and hospitality during my stay at the Australian Museum, and for facilitating the present study.

Diagnosis. Body smooth dorsally. Gills on pereonites 2–4. Antenna 1 shorter than half of the body. Distal article of the mandibular palp with 3–4 setae. Pereopods 3 and 4 absent. Pereopod 5 uniarticulate, present in males and females. Abdomen with two pairs of uniarticulate abdominal appendages.

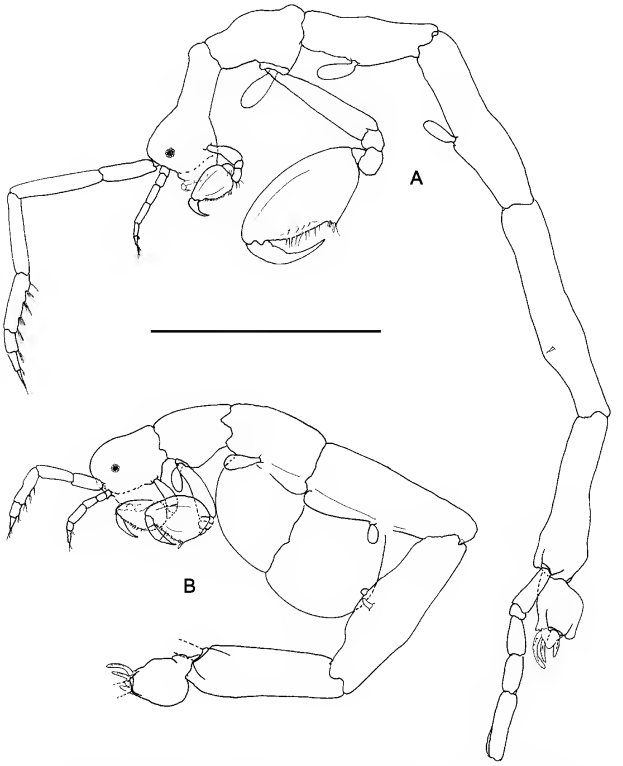


Fig. 7. *Hircella berentsae* n.sp. Lateral view. (*A*) holotype male (AM P61610); (*B*) paratype female (AM P61611). Scale: 1 mm.

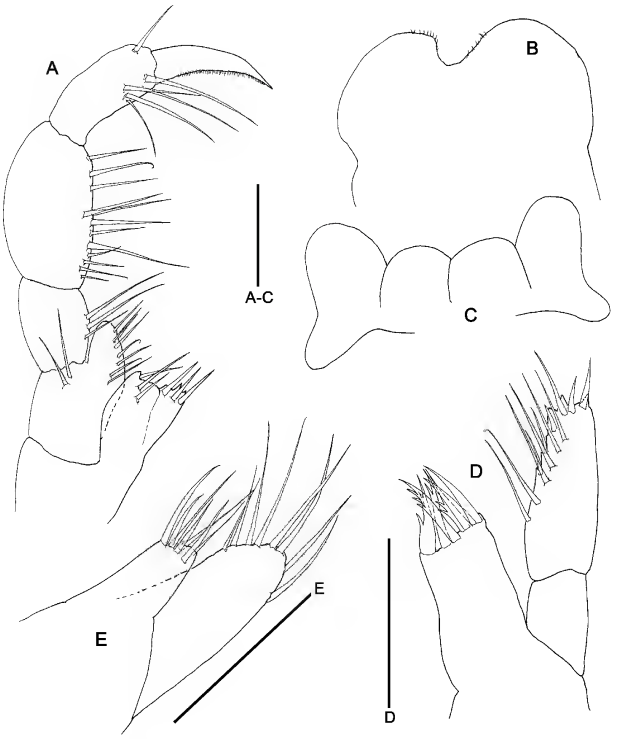


Fig. 8. *Hircella berentsae* n.sp. Holotype male (AM P61610). (*A*) maxilliped; (*B*) upper lip; (*C*) lower lip; (*D*) maxilla 1; (*E*) maxilla 2. Scales 0.05 mm.

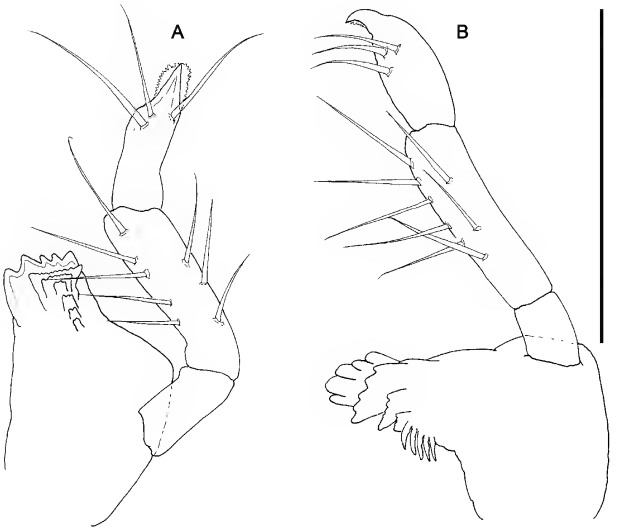


Fig. 9. *Hircella berentsae* n.sp. Holotype male (AM P61610). (*A*) right mandible; (*B*) left mandible. Scale: 0.1 mm.

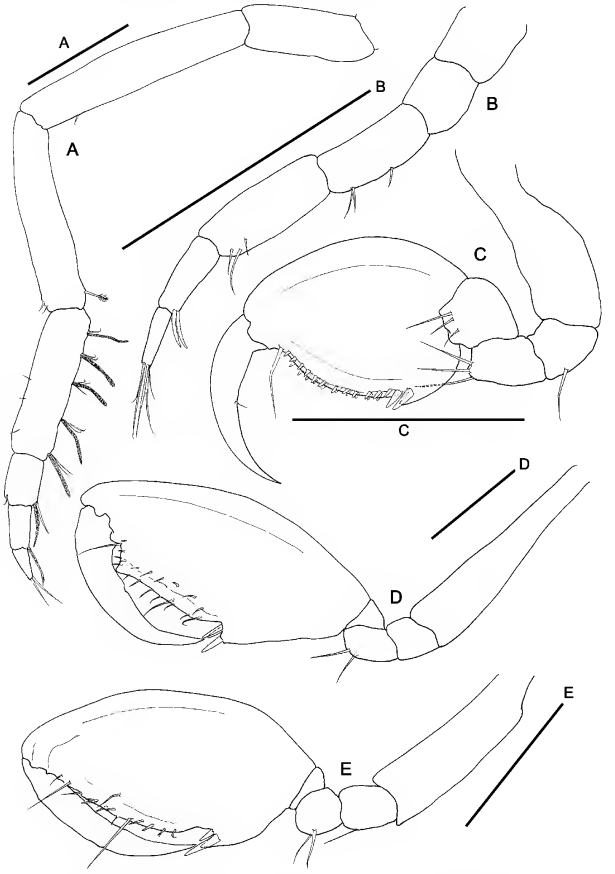


Fig. 10. *Hircella berentsae* n.sp. (*A–D*) holotype male (AM P61610). (*A*) antenna 1; (*B*) antenna 2; (*C*) gnathopod 1; (*D*) gnathopod 2; (*E*) paratype female (AM P61611) gnathopod 2. Scales 0.2 mm.

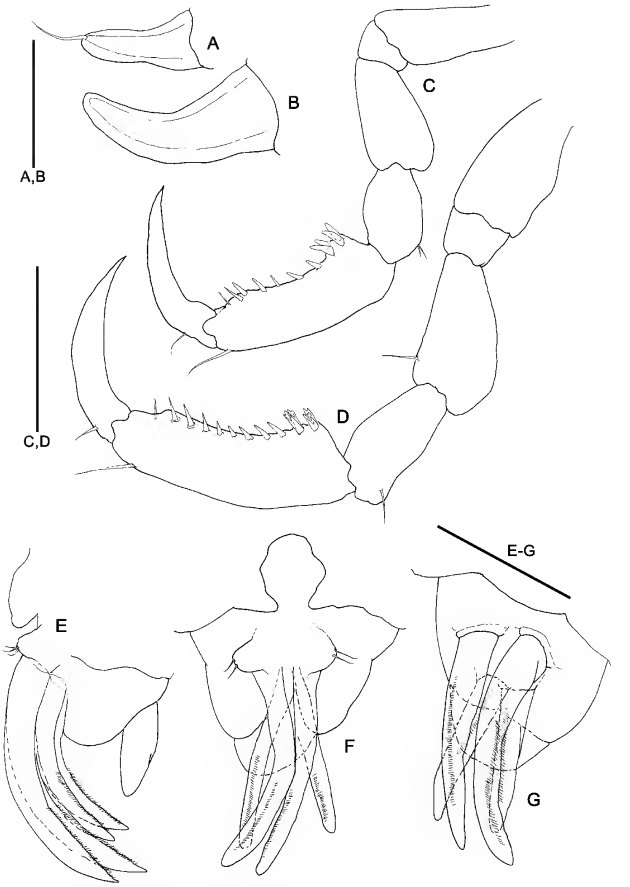


Fig. 11. *Hircella berentsae* n.sp. (*A,C–F*) holotype male (AM P61610); (*B,G*) paratype female (AM P61611). (*A,B*) pereopod 5; (*C*) pereopod 6; (*D*) pereopod 7; (*E*) abdomen (lateral view); (*F,G*) abdomen (ventral view). Scales: A,B: 0.2 mm; C,D: 0.3 mm; E–G: 0.1 mm.

Description

Holotype male. • *Body length* 3.7 mm. • *Lateral view* (Fig. 7A). Body dorsally smooth. Head rounded. Eyes small. Pereonite 1 fused with head, suture not present; pereonites 2–5 increasing in length; pereonite 7 shortest. • *Gills* (Fig. 7A). Present on pereonites 2–4, oval, length about two times width. Gills on pereonite 4 slightly shorter than those on pereonite 2 and 3. • *Mouthparts*. Upper lip (Fig. 8B) symmetrically bilobed, slightly pubescent apically. Mandibles (Fig. 9A,B) with 3-articulate palp; distal article of palp with three apical setae; second article with eight simple setae; mandibular molar absent; left mandible (Fig. 9B) with 5-toothed incisor, lacinia mobilis 5-toothed followed by a row of minutely serrated plates decreasing in size; incisor of right mandible (Fig. 9A) 5-toothed, lacinia mobilis deeply serrate, followed by a row of minutely serrate plates; molar flake absent. Lower lip (Fig. 8C) with inner lobes well demarcated; inner and outer lobes without setulae. Maxilla 1 (Fig. 8D) outer lobe with six robust setae, serrate laterally; distal article of palp with six apical setae and row of six setae medially. Maxilla 2 (Fig. 8E) inner lobe rectangular with seven setae distally; outer lobe oval, twice as long as inner lobe, with eight apical setae. Maxilliped (Fig. 8A) inner plate rectangular with six setae; outer plate smaller than the inner plate, with setae; palp four-articulate; dactylus with a row of setulae. • *Antennae*. Antenna 1 (Fig. 10A) robust, about one-third of body length; flagellum four-articulate. Antenna 2 (Fig. 10B) about one-third length of antenna 1; swimming setae absent; flagellum 2-articulate. • *Gnathopods*. Gnathopod 1 (Fig. 10C) basis

as long as ischium, merus and carpus combined; propodus oval, length about 1.2 times width, palm with pair of grasping spines proximally and two rows of smaller spines along palm; dactylus robust and curved, with short setae medially. Gnathopod 2 (Fig. 10D) inserted on the posterior half of pereonite 2; basis as long as pereonite 2; ischium rectangular; merus rounded; carpus short and triangular; propodus rectangular, about 1.2 times as long as basis; palm with three grasping spines proximally and distal projection; dactylus curved and narrowed distally, smooth. • *Pereopods*. Pereopod 5 (Fig. 11A) extremely reduced, with distal seta. Pereopods 6 and 7 (Fig. 11C,D) robust; basis without carina, ischium short and rectangular; propodus palm with two pairs of robust spines proximally and a row of smaller spines along occlusal margin. • *Penes* (Fig. 11E,F) situated laterally, length about 1.2 times width. • *Abdomen* (Fig. 11E,F) with pair of small projections, each with two setae distally (probably vestigial pleopods), two pairs of long uniarticulate appendages (uropods), and a single dorsal lobe.

Paratype female. • *Body length* 3.2 mm. Antenna 1 flagellum 3-articulate (Fig. 7B). Propodus palm of gnathopod 2 (Fig. 10E) without distal projection. Oostegites not setose (Fig. 7B). Pereopod 5 (Fig. 11B) twice as long as in male, without setae and curved. Abdomen (Fig. 11G) without small projections.

Remarks. Mayer (1882) established the genus *Hircella* mainly on the basis of the absence of pereopod 5. The genus *Liriarchus* Mayer, 1912 is also characterized by the absence of pereopod 5 in males or extremely reduced in females. However, *Hircella* and *Liriarchus* can be differentiated by the abdomen: two pairs of appendages are present in *Hircella* instead of one pair in *Liriarchus*. The present specimens collected from Queensland are assigned to *Hircella* on the basis of the presence of two pairs of appendages in the abdomen. *Hircella* presently includes *H. berentsae* n.sp., *H. cornigera* (Haswell, 1879), and *H. inermis* Guerra-García & Takeuchi, 2004, described from Tasmanian waters. *Hircella berentsae* n.sp. differs from *H. cornigera*, the type species of the genus, mainly on the basis of the following features: (1) pereopod 5 is present in females of *H. berentsae* but absent in females of *H. cornigera*; (2) the body is smooth in *H. berentsae* but provided with large dorsal acute projections on pereonites 3–5 in *H. cornigera*; and (3) antenna 1 is clearly shorter than half the body length in *H. berentsae* but longer in *H. cornigera*. Although *H. berentsae* n.sp. is closer to *H. inermis*, several constant differences indicate that both are valid species: (1) the adult body length of *H. inermis* is about 10 mm in contrast to 3–4 mm in *H. berentsae*; (2) pereopod 5 is absent in males of *H. inermis* but present in males of *H. berentsae*; (3) the antenna 1 flagellum is eight-articulate in males of *H. inermis* but four-articulate in *H. berentsae*; (4) the first pair of abdominal appendages is 2-articulate in *H. inermis* but one-articulate in *H. berentsae*; (5) the distal article of the mandibular palp bears six apical setae in *H. inermis* and 3 or 4 in *H. berentsae*.

Most morphological characters of *H. berentsae* are constant in all specimens examined. Nevertheless, the number of apical setae in the distal article of the mandibular palp varies, being three or four depending on the specimens.

Distribution. Elizabeth and Middleton Reefs, Tasman Sea, and Freshwater Bay, Queensland.

Hircella cornigera (Haswell, 1879)

Fig. 12

Caprella cornigera Haswell, 1879: 347–348, pl. 23: fig. 5.
Hircella cornigera Haswell, 1885: 999; Mayer, 1890: 16–17, pl. 5: figs. 10–11, pl. 6: figs 3–22; Mayer, 1903: 31–32; Stebbing, 1910: 652.

Material examined. 1♂, 1♀, AM P47048, Boat Rock, North Stradbroke Island, Queensland, 27°25.21'S 153°33.28'E, bryozoans, hydrozoans and brown algae, 28 m, 21.8°C, R.T. Springthorpe, 3 Jun 1993.

Remarks. In *H. cornigera*, pereopod 5 is reduced to a tiny article in males, and is absent in females. The type material of *Hircella cornigera* is lost (Springthorpe & Lowry, 1994).

Distribution. Previously known only from the type locality, Port Jackson, New South Wales, Australia (McCain & Steinberg, 1970); a new record for Queensland, Australia.

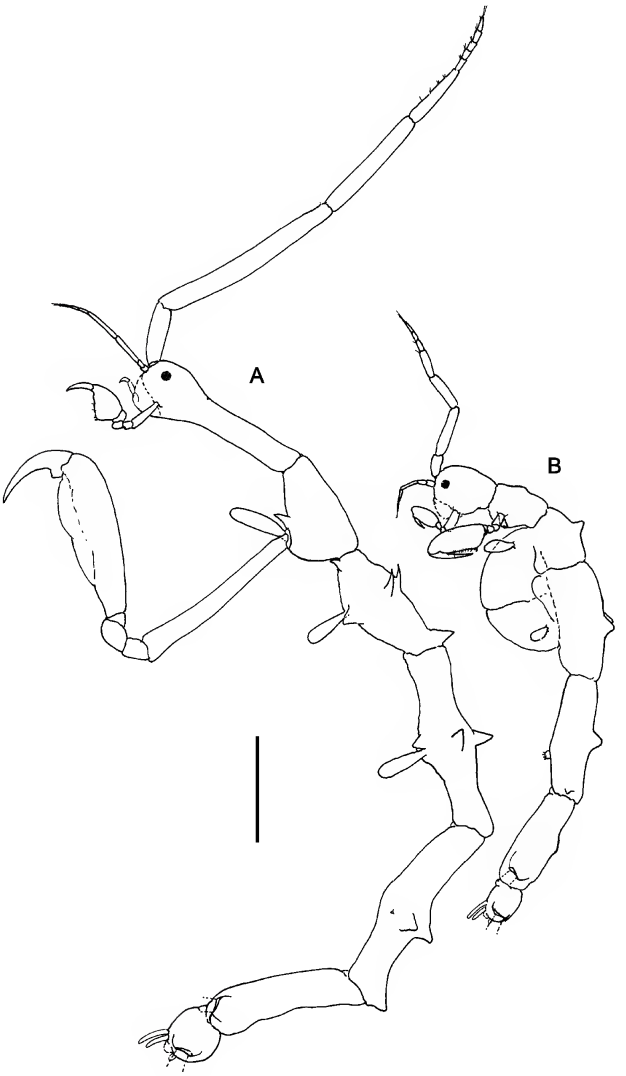


Fig. 12. *Hircella cornigera* (Haswell, 1879). Lateral view. (*A*) male; (*B*) female. (AM P47048). Scale: 1 mm.

Jigurru n.gen.

Diagnosis. Antenna 2 flagellum 2-articulate. Gills present on pereonites 2–4. Pereopods 3 and 4 absent. Pereopod 5 3-articulate, with basal article almost divided at midlength. Pereopods 6 and 7 six-articulate; carpus and propodus with a row of large spines along palm. Mandibular palp 3-articulate. Molar absent. Inner plates of maxilliped partially fused. Abdomen with two pairs of appendages.

Etymology. Named "Jigurru", the name given to Lizard Island by the traditional custodians of the island, the Dingaal people. Gender: masculine.

Type species. *Jigurru vailhoggett* n.sp.

Remarks. The new genus *Jigurru* shares some characters with *Caprellina* (Nicolet, 1849) and *Prellicana* Mayer, 1903. *Jigurru* appears to be closer to *Caprellina* than *Prellicana* on the basis of the presence of three pairs of gills, reduced pereonite 5 and two pairs of appendages in the abdomen. Nevertheless, the small size, general features of the body, the incomplete articulation of the basal article in the pereopods 5, the shape of pereopods 6 and 7, and the partially fused inner plates of the maxilliped strongly resemble *Prellicana*. *Prellicana*, however, has only two pairs of gills and one pair of abdominal appendages whereas *Jigurru* possesses three pairs of gills and two pairs of abdominal appendages.

Jigurru vailhoggett n.sp.

Figs 13–17

Type material. HOLOTYPE ♂, AM P61744, Coconut Beach, Lizard Island, Queensland, Australia, 14°40'S 145°28'E, dead thick branching hard coral encrusted with calcareous red algae and filamentous algal turf, 8 m, QLD 1475, J.M. Guerra-García & S.J. Keable, 8 Oct 2001. PARATYPES: 2♂♂, 1♀, AM P61745, type locality.

Etymology. The specific name is derived from "Vail" and "Hoggett" to dedicate the species to Lyle Vail and Anne Hoggett, directors of the Lizard Island Research Station for their help and kindness during the field study at Lizard Island; used as a noun in apposition.

Diagnosis. As for the genus.

Description

Holotype male. • *Body length*. 3.1 mm. • *Lateral view* (Fig. 13B). Body smooth without projections; head rounded; suture between head and pereonite 1 absent; pereonites 2–5 increasing in size respectively; pereonite 7 the shortest. • *Gills* (Fig. 13B). Present on pereonites 2–4, oval, length about 2 times width. • *Mouthparts*. Upper lip (Fig. 14B) symmetrically bilobed, lobes poorly demarcated, smooth apically. Mandibles (Fig. 15A,B) without molar; left mandible (Fig. 15B) with incisor 5-toothed, lacinia mobilis 5-toothed followed by a row of plates decreasing in size; right mandible (Fig. 15A) with incisor 5-toothed, lacinia mobilis with 2 teeth and serrate, followed by row of plates;

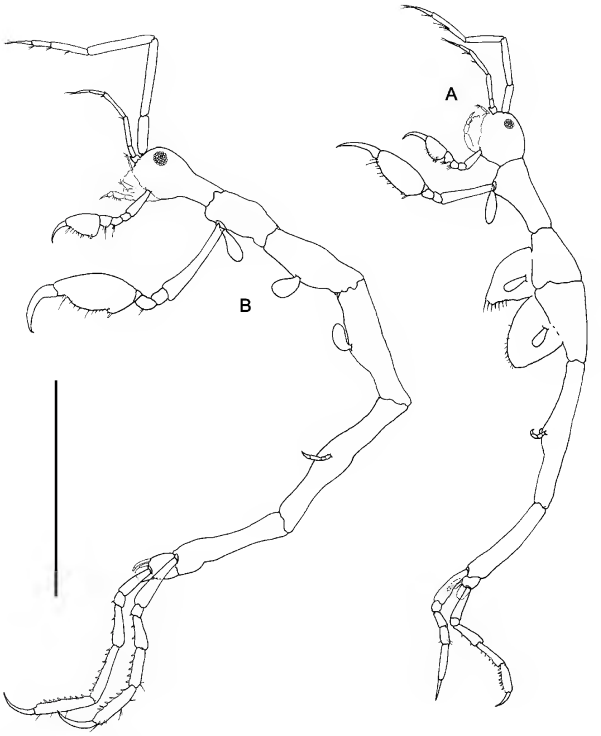


Fig. 13. *Jigurru vailhoggett* n.gen., n.sp. Lateral view. (*A*) paratype female (AM P61745); (*B*) holotype male (AM P61744). Scale: 1 mm.

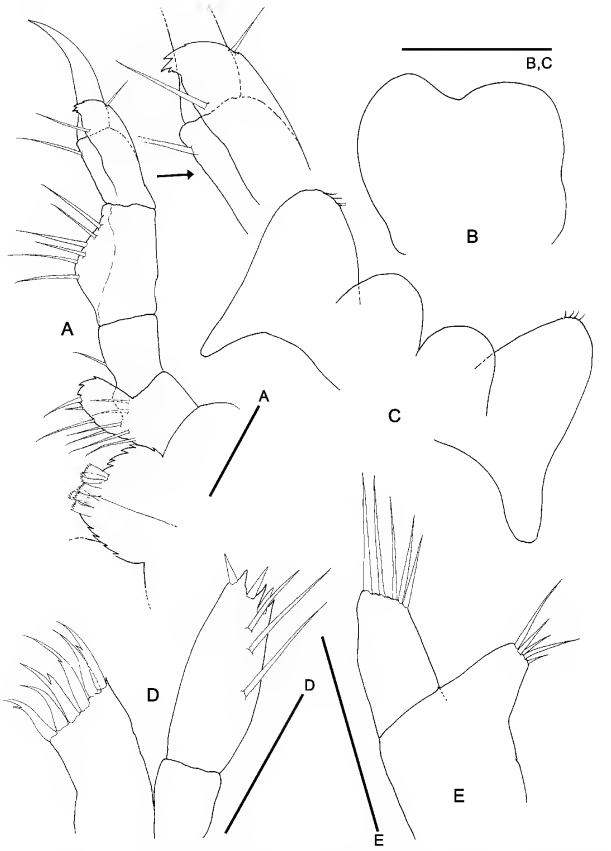


Fig. 14. *Jigurru vailhoggett* n.gen., n.sp. Holotype male (AM P61744). (*A*) maxilliped; (*B*) upper lip; (*C*) lower lip; (*D*) maxilla 1; (*E*) maxilla 2. Scales 0.05 mm.

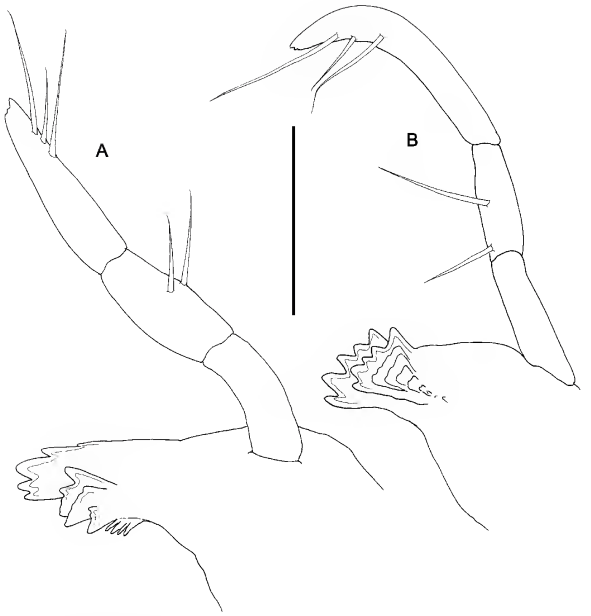


Fig. 15. *Jigurru vailhoggett* n.gen., n.sp. Holotype male (AM P61744). (*A*) right mandible; (*B*) left mandible. Scale: 0.05 mm.

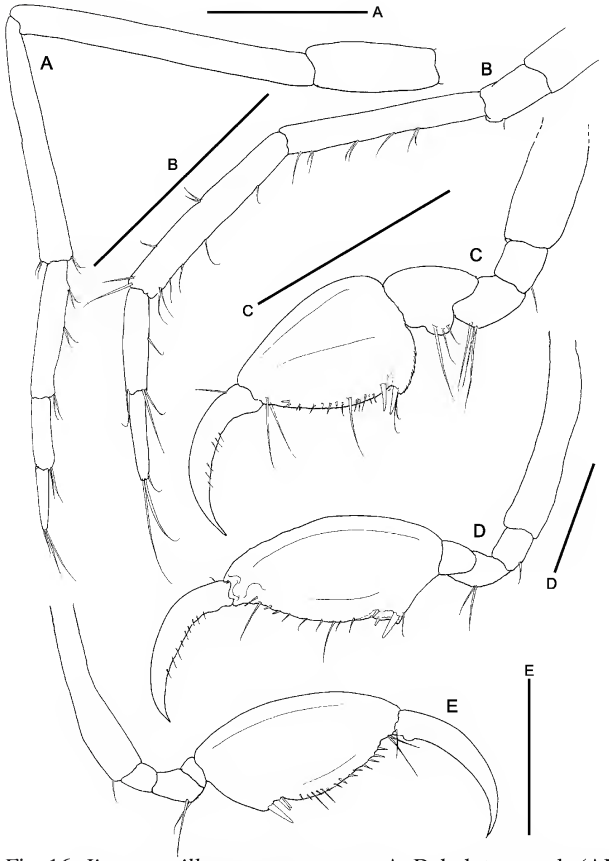


Fig. 16. *Jigurru vailhoggett* n.gen., n.sp. A–D, holotype male (AM P61744). (*A*) antenna 1; (*B*) antenna 2; (*C*) gnathopod 1; (*D*) gnathopod 2; (*E*) paratype female (AM P61745) gnathopod 2. Scales 0.2 mm.

palp 3-articulate, second article with two setae, distal article with three setae (formula 1-x-1, being x=1). Lower lip (Fig. 14C) with inner lobes well demarcated; outer lobes with some fine and short apical setae. Maxilla 1 (Fig. 14D) outer lobe with six robust and stout setae; distal article of palp

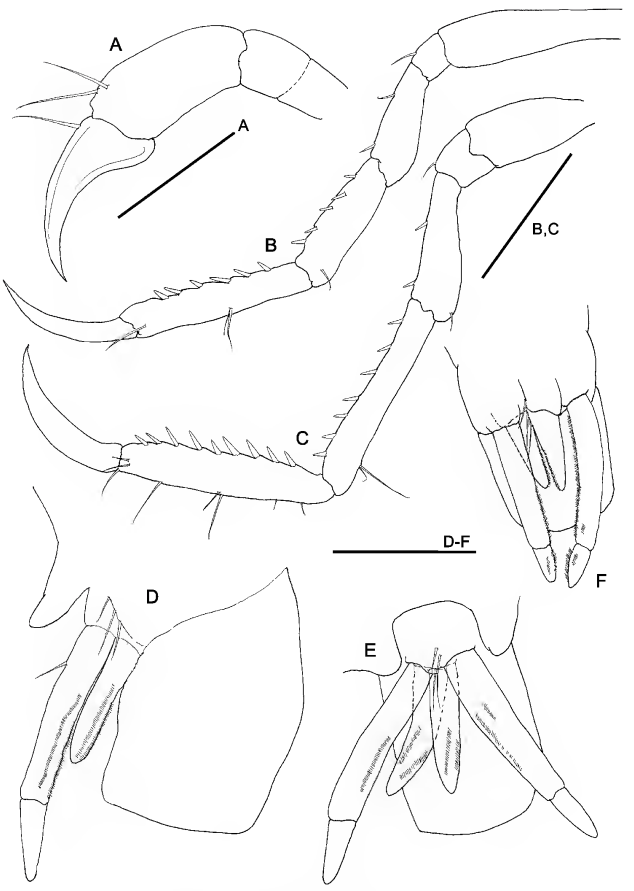


Fig. 17. *Jigurru vailhoggett* n.gen., n.sp. A–E, holotype male (AM P61744). (*A*) pereopod 5; (*B*) pereopod 6; (*C*) pereopod 7; (*D*) abdomen (lateral view); (*E*) abdomen (ventral view); (*F*) paratype female (AM P61745) abdomen (ventral view). Scales: A,D–F: 0.05 mm; B,C: 0.2 mm.

with three setae and three teeth distally and row of three lateral setae. Maxilla 2 (Fig. 14E) inner lobe triangular with five setae; outer lobe rectangular with five setae. Maxilliped (Fig. 14A) inner plates almost fused, with a serrate margin and three apically serrate nodular setae; outer plate with seven simple setae and serration; palp four-articulate, article 2 laterally expanded, with six setae; article 3 with large rectangular projection emerging from the base, with two setae laterally, serrate distally. • *Antennae*. Antenna 1 (Fig. 16A) about ⅓ of the body length; flagellum 3-articulate. Antenna 2 (Fig. 16B) a little shorter than the half of the antenna 1, sparsely setose; swimming setae absent; flagellum 2-articulate. • *Gnathopods*. Gnathopod 1 (Fig. 16C) basis as long as ischium, merus and carpus combined; ischium rectangular; merus rounded; propodus triangular, length about 1.5 times width, palm with three proximal grasping spines, grasping margin minutely denticulate on anterior half; dactylus elongate and curved, provided with long seta dorsally, and a row of short setae ventrally. Gnathopod 2 (Fig. 16D) inserted on the anterior part of pereonite 2; basis about 1.2 times as long as pereonite 2; ischium rectangular; merus rounded; carpus triangular; propodus oval, length about 2 times width, palm with three proximal grasping spines; dactylus curved, with row of short setae. • *Pereopods*. Pereopods 3 and 4 absent (Fig. 13B). Pereopod 5 3-articulate (Fig. 17A), but basal article almost divided into two articles. Pereopods 6 (Fig. 17B) and 7 (Fig.

17C), six-articulate, ischium with one seta, merus with two spines, carpus with five (pereopod 6) or seven (pereopod 7) spines along the palm, carpus with six (pereopod 6) or nine (pereopod 7) spines, dactylus smooth. • *Penes* (Fig. 17D,E) large, triangular, as long as wide, small suture present apically. Abdomen (Fig. 17D,E) with two pair of appendages and a large, prismatic dorsal lobe; first pair of appendages 2-articulate; second pair uniarticulate.

Paratype female. • *Body length* 2.2 mm. Oostegites (Fig. 13A) scarcely setose. Gnathopod 2 (Fig. 16E) similar to male, but with dactylus slightly more elongate.

Remarks. The maxilliped of *Jigurru vailhoggett* n.sp. is close to the maxilliped of *Prellicana minima* Mayer, 1903 on the basis of the inner plates, being partially fused. However, the lateral expansion on article 2 and the well-developed projection on article 3 are present, so far, only in *Jigurru vailhoggett* n.sp in the subfamily Phtisicinae.

Distribution. Lizard Island, Queensland.

Mayericaprella n.gen.

Diagnosis. Flagellum of antenna 2 2-articulate. Gills present on pereonites 2–4. Pereopods 3 and 4 absent. Pereopod 5 four-articulate. Pereopods 6 and 7 six-articulate; propodus with two pairs of proximal grasping spines. Mandibular palp 3-articulate. Molar absent. Abdomen with two pairs of 2-articulate appendages.

Etymology. *Mayericaprella* is derived from "Mayer" and "*Caprella*" to dedicate the genus to P. Mayer for his valuable contributions to the knowledge of the Caprellidae during the last century. Gender: feminine.

Type species. *Mayericaprella arimotoi* n.sp.

Remarks. *Mayericaprella* n.gen. is close to *Caprellina*, especially to *Caprellina bispinosa* Müller, 1990. The general shape of the body, the structure of the antennae, the distribution of the gills, the mouthparts (especially the maxilliped) and the abdomen are similar to that of species of *Caprellina*. However, the gnathopods and pereopods are different, especially pereopod 5 which is four-articulate in the new genus and 2- or 3-articulate in *Caprellina* (2-articulate in *C. bispinosa* and 3-articulate in *C. longicollis* and *C. spiniger*). The only other genus in the subfamily Phtisicinae with four-articulate pereopods 5 is *Quadrisegmentum*. Although *Mayericaprella* shares with *Quadrisegmentum* the presence of four-articulate pereopod 5, the genera differ chiefly in pereopods 3 and 4, being present in the latter and absent in former. The number of articles on pereopod 5 is an important phylogenetic character in the Phtisicinae because they show progressive changes in segmentation of the limb (Hirayama, 1988). At present, the number of articles in the pereopods distinguishes genera (Mayer, 1903; Arimoto, 1976). For instance, genera close to *Caprellina*, such as *Hircella*, have been erected mainly on the basis of one-articulate pereopod 5. Nevertheless, Müller (1990) assigned *C. bispinosa* (having a 2-articulate pereopod 5) to *Caprellina* (characterized by a 3-articulate pereopod 5) instead of erecting a new genus for the species. Further study might show that *C. bispinosa* should be transferred to a different genus. The general morphology of *Mayericaprella*, with a four-articulate pereopod 5, is closer to *Caprellina bispinosa* with pereopod 5 2-articulate, than to the remaining species of *Caprellina* with a 3-articulate pereopod 5. Actually, the phylogenetic relationships among the species of the seemingly closely related genera *Caprellina, Pseudocaprellina, Hircella* and *Liriarchus* require study. The continuous gradient of variation in the characters of species of these genera makes generic distinctions difficult. A complete phylogenetic revision of the Caprellidae, necessary to address properly future taxonomic studies of this group, is required.

Mayericaprella arimotoi n.sp.

Figs 18–22

Type material. HOLOTYPE ♂, AM P61561, outer slope, W of "Yoshin Maru Iwaki", Elizabeth Reef, Australia, 29°57.2'S 159°01.2'E, coral rubble, 8–24 m, st 30, J.K. Lowry & R.T. Springthorpe, 12 Dec 1987. PARATYPES: 1♀, AM P61562, type locality; 1♀, AM P61563, type locality; 1♂, 2♀♀, AM P61565, reef flat near "Yoshin Maru Iwaki", Elizabeth Reef, Australia, 29°57.2'S 159°01.2'E, J.K Lowry & R.T. Springthorpe, st 43, 14 Dec 1987; 1♂, AM P61566, large alcove near lagoon entrance, Sound dive site, Middleton Reef, Australia, 29°27.7'S 159°05.4'E, 6 m, P. Hutchings & I. Loch, st 7, 5 Dec 1987.

Etymology. The species is dedicated to I. Arimoto for his valuable taxonomic studies on the Caprellidae.

Diagnosis. As for the genus.

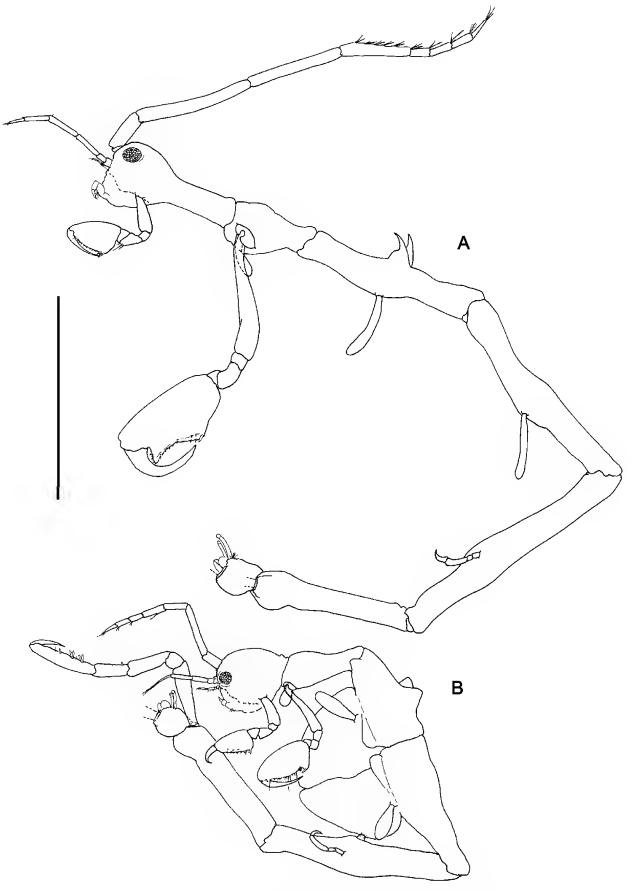


Fig. 18. *Mayericaprella arimotoi* n.gen., n.sp. Lateral view. (*A*) holotype male (AM P61561); (*B*) paratype female (AM P61562). Scale: 1 mm.

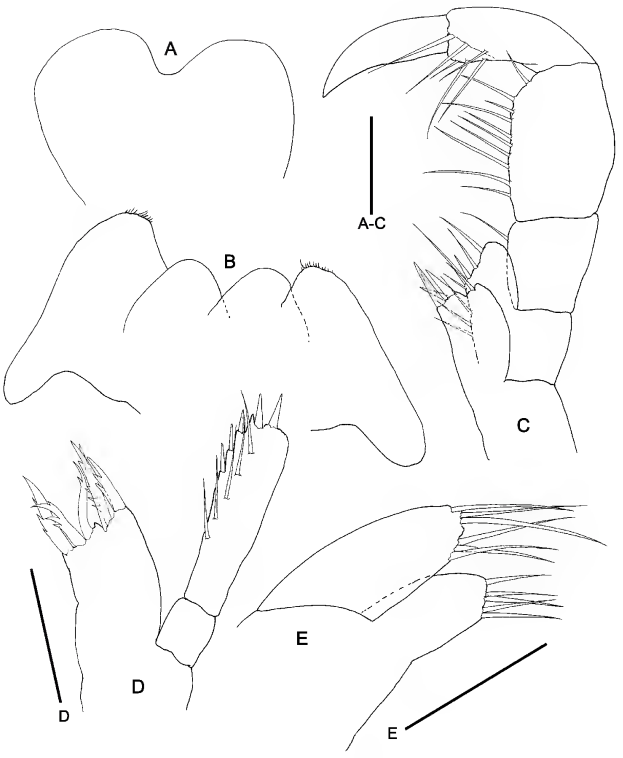


Fig. 19. *Mayericaprella arimotoi* n.gen., n.sp. Holotype male (AM P61561). (*A*) upper lip; (*B*) lower lip; (*C*) maxilliped; (*D*) maxilla 1; (*E*) maxilla 2. Scales 0.05 mm.

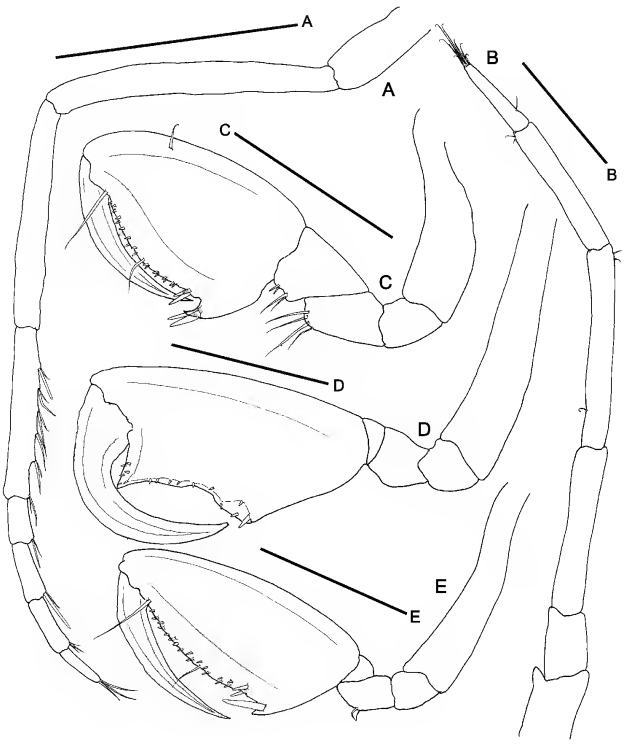


Fig. 21. *Mayericaprella arimotoi* n.gen., n.sp. A–D, holotype male (AM P61561). (*A*) antenna 1; (*B*) antenna 2; (*C*) gnathopod 1; (*D*) gnathopod 2; (*E*) paratype female (AM P61562) gnathopod 2. Scales: A: 0.5 mm; B: 0.1 mm; C,E: 0.2 mm; D: 0.3 mm.

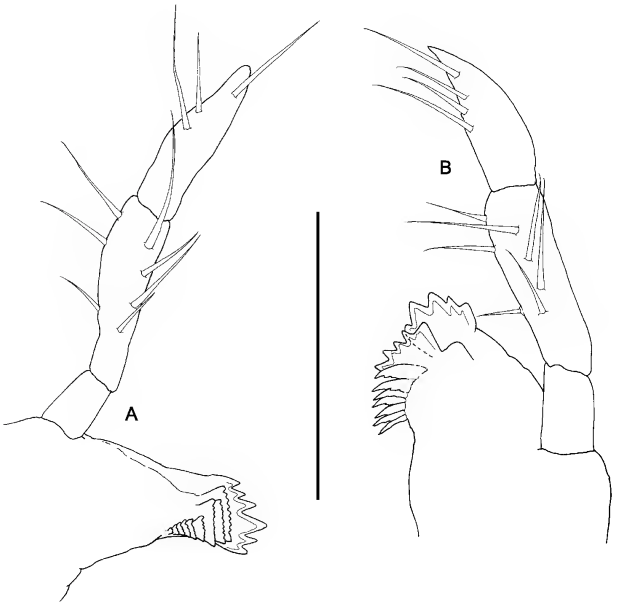


Fig. 20. *Mayericaprella arimotoi* n.gen., n.sp. Holotype male (AM P61561). (*A*) right mandible; (*B*) left mandible mandible. Scale: 0.1 mm.

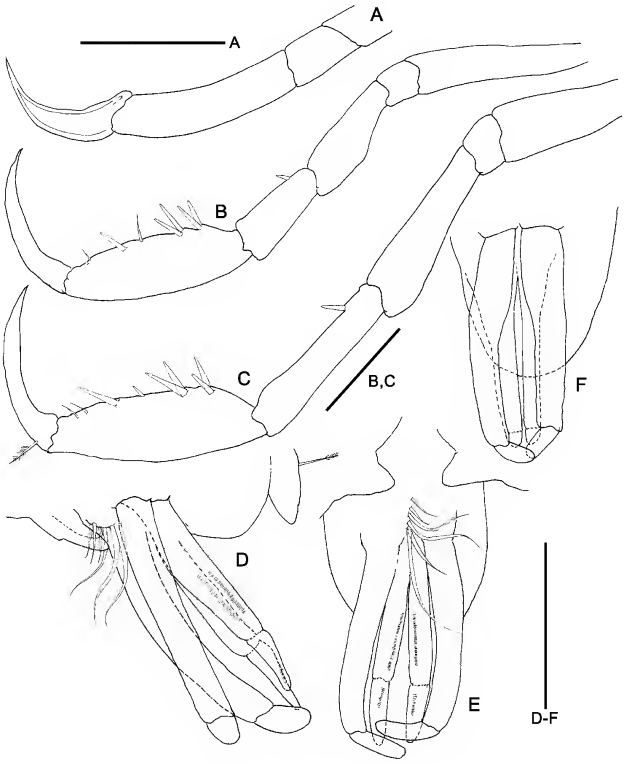


Fig. 22. *Mayericaprella arimotoi* n.gen., n.sp. (*A–E*) holotype male (AM P61561). (*A*) pereopod 5; (*B*) pereopod 6; (*C*) pereopod 7; (*D*) abdomen (lateral view); (*E*) abdomen (ventral view); (*F*) paratype female (AM P61562) abdomen (ventral view). Scales 0.1 mm.

Description

Holotype male. • *Body length*. 5.2 mm. • *Lateral view* (Fig. 18A). Body smooth except for a pair of acute projections on the middle of the pereonite 3; head rounded; suture between head and pereonite 1 absent; pereonites 2–5 increasing in size respectively; pereonite 7 the shortest. • *Gills* (Fig. 18A). Present on pereonites 2–4. Gills on pereonite 2 oval, 2.5 times as long as wide. Gills on pereonites 3 and 4 elongate, length about 4 times width. • *Mouthparts*. Upper lip (Fig. 19A) symmetrically bilobed, smooth apically. Mandibles (Fig. 20A,B) without molar; left mandible (Fig. 20B) with incisor and lacinia mobilis 5-toothed, followed by a row of plates decreasing in size; right mandible (Fig. 20A) with incisor 6-toothed, lacinia mobilis transformed into a plate minutely serrate distally, followed by row of similar plates decreasing in size; palp 3-articulate, second article with seven setae, distal article with setal formula 1-x-1, being x=1 in the right mandible and 2 in the left one. Lower lip (Fig. 19B) with inner lobes well demarcated; outer lobes with some fine and short setulae apically. Maxilla 1 (Fig. 19D) outer lobe with six robust serrate setae; distal article of the palp with five setae distally and five setae laterally. Maxilla 2 (Fig. 19E) inner lobe rectangular with five setae; outer lobe rectangular about 1.2 times as long as inner lobe, with six setae. Maxilliped (Fig. 19C) inner plate with three robust setae and a slender seta; outer plate with eight simple setae; palp four-articulate, dactylus smooth. • *Antennae*. Antenna 1 (Fig. 21A) about ⅔ body length; flagellum five-articulate. Antenna 2 (Fig. 21B) about ⅓ length of the antenna 1, scarcely setose; swimming setae absent; flagellum 2-articulate. • *Gnathopods*. Gnathopod 1 (Fig. 21C) basis as long as ischium, merus and carpus combined; ischium rectangular; merus rounded; carpus trapezoidal; propodus oval, length about 1.5 times width; palm with acute proximal projection with pair of proximal grasping spines, followed by another pair of proximal grasping spines, and two rows of smaller spines along palm; dactylus slightly curved and smooth. Gnathopod 2 (Fig. 21D) inserted on anterior part of pereonite 2; basis about 1.5 times as long as pereonite 2; ischium and merus rectangular; carpus short and triangular; propodus as long as the basis, length about 2 times width; palm with rows of small grasping spines and a well-developed triangular projection distally; dactylus robust, strongly curved, smooth. • *Pereopods*. Pereopod 3 and 4 absent (Fig. 18A). Pereopod 5 four-articulate (Figs 18A, 22A). Pereopods 6 (Fig. 22B) and 7 (Fig. 22C) six-articulate; carpus with a grasping spine; propodus with two pairs of proximal grasping spines, followed by a setae, another grasping spine and two setae distally; dactylus of pereopod 7 with a plumose seta. • *Penes* (Fig. 22D,E) triangular, as long as wide. • *Abdomen* (Fig. 22D,E) with two pairs of 2-articulate appendages and a dorsal lobe with two plumose setae; a row of setae present between the penes and the appendages.

Paratype female. • *Body length* 3.6 mm. Oostegites (Fig. 18B) not setose. Projections on pereonite 3 rounded. Gnathopod 2 (Fig. 21E) with three proximal grasping spines, without triangular projection distally. Abdomen (Fig. 22F) without row of setae between the penes and appendages.

Remarks. The new species strongly resembles *Caprellina bispinosa* Müller, 1990. Nevertheless both species can be easily distinguished by the segmentation of pereopod 5, being 2-articulate in *C. bispinosa*, and four-articulate in *Mayericaprella arimotoi*.

Distribution. Presently known from Elizabeth and Middleton Reefs, Tasman Sea.

Metaproto Mayer, 1903

Metaproto novaehollandiae (Haswell, 1880)

Fig. 23

Proto novae-hollandiae Haswell, 1880: 275–276, pl. 2: fig. 3; Mayer, 1882: 26; Stebbing, 1888: 1230–1232; Mayer 1890: 14–15.
Metaproto novaehollandiae Mayer, 1903: 26–27, pl. 1: figs. 11–12, pl. 6: figs. 24–28, pl. 9: figs 3, 50; Stebbing, 1910: 651–652; McCain & Steinberg, 1970: 56; Laubitz, 1991: 103–104, fig. 1.

Material examined. 3♀♀, AM P61619 (QLD 683); 1♂, 1 juvenile, AM P61618 (QLD 686); 3♂♂, 2♀♀, AM P32303 (GBR 6); 2♂♂, AM P32309 (GBR 14); 1♂, 2♀♀, AM P32330 (GBR 56); 2♀♀, AM P32332 (GBR 63); 1♂, AM P32277 (GBR 68); >20 specimens, AM P61695 (QLD 1486); >20 specimens, AM P61696 (QLD 1523); 1♂, AM P61697 (QLD 1535); 3♂♂, 5♀♀, 1 juvenile, AM P61698 (QLD 1538); 1♀, AM P61699 (QLD 1563); 1♂, AM P61700 (QLD 1571); 6♂♂, 7♀♀, AM P61701 (QLD 1572); >20 specimens, AM P61702 (QLD 1574); >20 specimens, AM P61703 (QLD 1575).

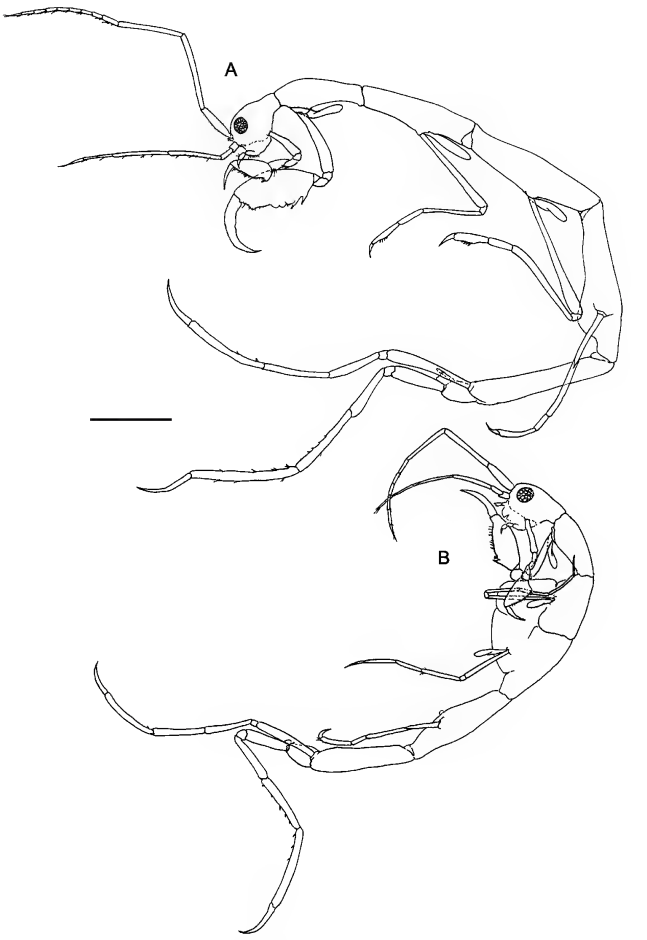


Fig. 23. *Metaproto novaehollandiae* (Haswell, 1880). Lateral view. (*A*) male; (*B*) female. (AM P61702). Scale: 1 mm.

Remarks. *Metaproto* can be easily distinguished from all other genera of the Phtisicinae by the presence of only one pair of abdominal appendages. The specimens examined here are in good agreement with those described by Haswell (1880) and redescribed by Mayer (1903) and Laubitz (1991), and with AM specimens collected from Philippines and Papua New Guinea reported by Guerra-García (2002a, 2003). This species was recorded from Queensland by Jones (1984) as *Phtisica marina*.

Distribution. Port Jackson, New South Wales, Australia (Haswell, 1880), Banda Sea, Indonesia, South Africa (McCain & Steinberg, 1970), New Caledonia and Philippines (Laubitz, 1991; Guerra-García, 2002a), and Papua New Guinea (Guerra-García, 2003).

Perotripus Dougherty & Steinberg, 1953

Perotripus keablei n.sp.

Figs 24–27

Type material. HOLOTYPE ♂, AM P61747, off Mangrove Beach, Lizard Island, Queensland, 14°40'S 145°28'E, sand, 1.5 m, GBR 6, C. Short & A.R. Jones, 30 Sep 1978. PARATYPES (all Lizard Island, Queensland): 1♀, AM P61748, between Bird Islet & Trawler Beach, 14°40'S 145°28'E, sand, 15 m, GBR 14, J.K. Lowry & P.C. Terrill, 5 Oct 1978; 1♀, AM P32295, Lagoon, 14°41'S 145°28'E, 1.5 m, GBR 5, C. Short & P.C. Terrill, 30 Sep 1978; 3♂♂, 4♀♀, AM P32304, type locality; 1♀, AM P32293, between Mangrove Beach & South Island, 14°40'S 145°28'E, sand, 9 m, GBR 7, J.K. Lowry & P.C. Terrill, 30 Sep 1978; 1♀, AM P32297, off S end Casuarina Beach, 14°40'S 145°28'E, beach sand, low water mark, GBR 10, J.K. Lowry, 4 Oct 1978; 5♂♂, 6♀♀, AM P61749, type locality; 1 premature ♀, AM P32298, between Bird Islet & South Island, 14°40'S 145°28'E, coral rubble, 21 m, GBR 15, A.R. Jones, 7 Oct 1978; 1♀, AM P32294, Mermaid Cove, 14°41'S 145°28'E, sand between corals, 6 m, GBR 26, C. Short & P.C. Terrill, 8 Oct 1978; 1♀, AM P32296, Between Bird Islet & South Island, 14°41'S 145°28'E, sediment at reef base with mixed algae, 25 m, GBR 29, J.K. Lowry, 9 Oct 1978; 1♂, AM P61750, Blue Lagoon, between Bird Islet and South Island, sediment (medium grained sand), 6 m, QLD 1538, J.M. Guerra-García & S.J. Keable, 13 Oct 2001.

Etymology. Named after Stephen Keable, Australian Museum, for his assistance during the sampling at Lizard Island and for his encouragement, advice, help and friendship during my stay at the Australian Museum.

Diagnosis. Body dorsally smooth. Gills on pereonites 2–4. Flagellum of antenna 1 2-articulate. Pereopods 3 and 4 uniarticulate. Pereopod 5 with 3 articles. Abdomen without appendages.

Description

Holotype male. • *Body length*. 5.2 mm. • *Lateral view* (Fig. 24A). Body dorsally smooth. Head rounded. Pereonite 1 fused with head, suture almost absent; pereonites 2 and 3 rounded; pereonites 4–6 elongate; pereonites 5 and 6 subequal in length; pereonite 7 the shortest. • *Gills* (Fig.

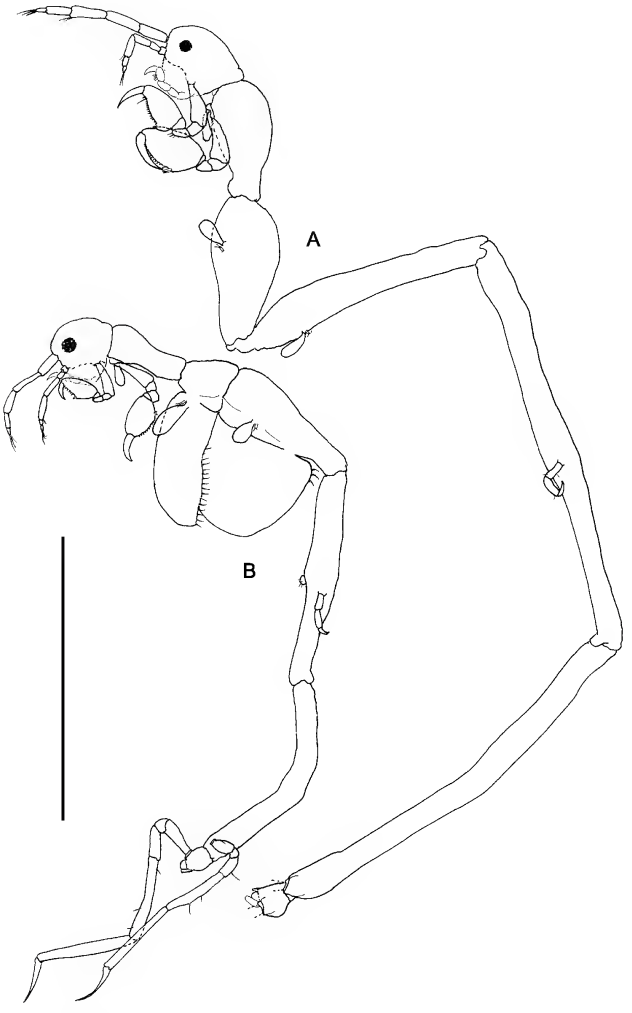


Fig. 24. *Perotripus keablei* n.sp. Lateral view. (*A*) holotype male (AM P61747); (*B*) paratype female (AM P61748). Scale: 1 mm.

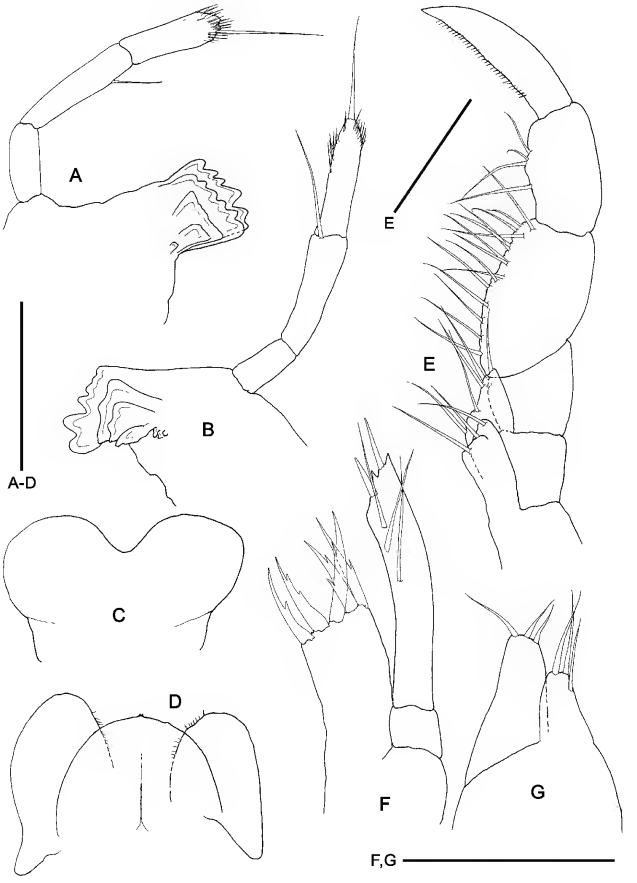


Fig. 25. *Perotripus keablei* n.sp. Holotype male (AM P61747). (*A*) left mandible; (*B*) right mandible; (*C*) upper lip; (*D*) lower lip; (*E*) maxilliped; (*F*) maxilla 1; (*G*) maxilla 2. Scale: 0.05 mm.

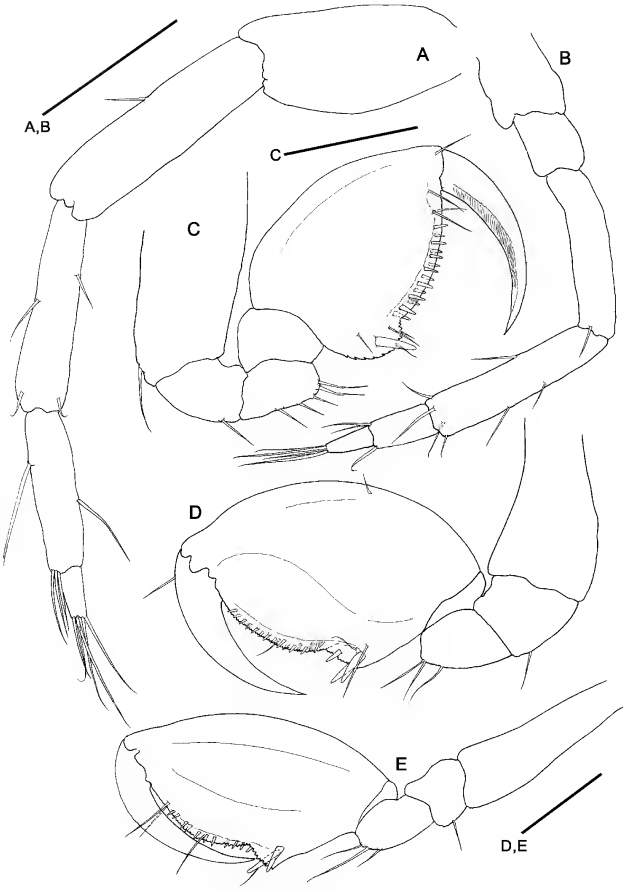


Fig. 26. *Perotripus keablei* n.sp. (*A–D*) holotype male (AM P61747). (*A*) antenna 1; (*B*) antenna 2; (*C*) gnathopod 1; (*D*) gnathopod 2; (*E*) paratype female (AM P61748) gnathopod 2. Scales 0.1 mm.

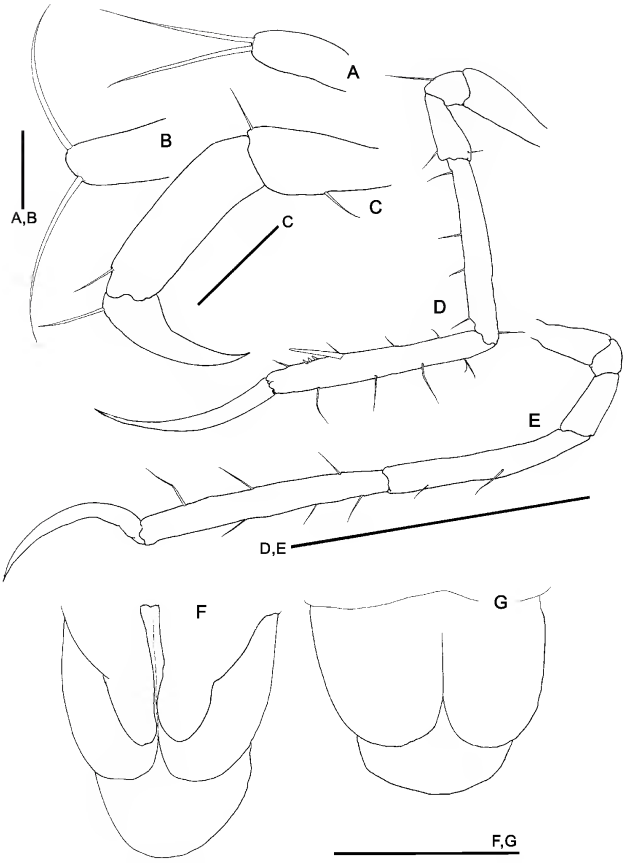


Fig. 27. *Perotripus keablei* n.sp. (*A–C,F*) holotype male (AM P61747); (*D,E*) paratype male (AM P61749). (*A*) pereopod 4; (*B*) pereopod 3; (*C*) pereopod 5; (*D*) pereopod 6; (*E*) pereopod 7; (*F*) abdomen (ventral view); (*G*) paratype female (AM P61748) abdomen (ventral view). Scales (mm): A,B: 0.02; C,F,G: 0.05; D,E: 0.5 mm.

24A). Present on pereonites 2–4, oval, length about two times width. • *Mouthparts*. Upper lip (Fig. 25C) symmetrically bilobed, smooth apically. Mandibles (Fig. 25A,B) with 3-articulate palp; distal article of palp with one simple apical seta and minute setulae distally; second article with a simple setae; mandibular molar absent; left mandible (Fig. 25A) with 6-toothed incisor, lacinia mobilis 6-toothed followed by three plates decreasing in size respectively; incisor of right mandible (Fig. 25B) 6-toothed, lacinia mobilis transformed into a plate, followed by four more plates decreasing in size respectively. Lower lip (Fig. 25D) with inner lobes fused, forming a semicircular plate; outer lobes with some setulae distally. Maxilla 1 (Fig. 25F) outer lobe with five robust setae, serrate laterally; distal article of the palp with two apical setae and row of three setae medially. Maxilla 2 (Fig. 25G) inner lobe with 3 distal setae; outer lobe about 1.3 times as long as inner lobe, with 3 setae. Maxilliped (Fig. 25E) inner plate rectangular, with three setae distally; outer plate triangular, as long as inner plate; palp four-articulate, dactylus with a row of setulae. • *Antennae*. Antenna 1 (Fig. 26A) about 1/12 body length; flagellum 2-articulate. Antenna 2 (Fig. 26B) about ⅔ length of antenna 1; swimming setae absent; flagellum 2-articulate. • *Gnathopods*. Gnathopod 1 (Fig. 26C) basis as long as the ischium, merus and carpus combined; propodus oval, length about 1.2 times width, palm serrate proximally with a grasping spines and two rows of smaller spines along the palm; dactylus elongate and slightly curved, smooth. Gnathopod 2 (Fig. 26D) inserted on anterior half of pereonite 2 (Fig. 24A); basis length one-half of pereonite 2; ischium rectangular; merus rounded; carpus short and triangular; propodus oval, about 1.3 times as long as basis; palm with three grasping spines proximally and two rows of smaller spines along palm; dactylus short and slightly curved, with dorsal seta proximally. • *Pereopods*. Pereopods 3 and 4 (Fig. 27A,B) subequal, small and one-articulate, with two setae distally. Pereopod 5 (Fig. 27C) 3-articulate and sparsely setose. Pereopods 6 and 7 six-articulate (Fig. 27D,E). Propodus of pereopod 6 with large spine followed by three smaller spines, distally robust, propodus of pereopod 7 without spines (missing in holotype, described from a male paratype). • *Penes* (Fig. 27F) positioned medially, large, length about 2.5 times width. • *Abdomen* (Fig. 27F) without projections except for two lateral lobes and one dorsal lobe.

Paratype female. • *Body length* 2.7 mm. Pereonites 4–6 (Fig. 24B) shorter than in male; propodus of gnathopod 2 (Fig. 26E) twice as long as wide. Oostegites sparsely setose (Fig. 24B). Palm of pereopod 6 without spines (Fig. 24B).

Remarks. The only other known species of *Perotripus* is *P. brevis* (La Follette, 1915) from the west coast of North

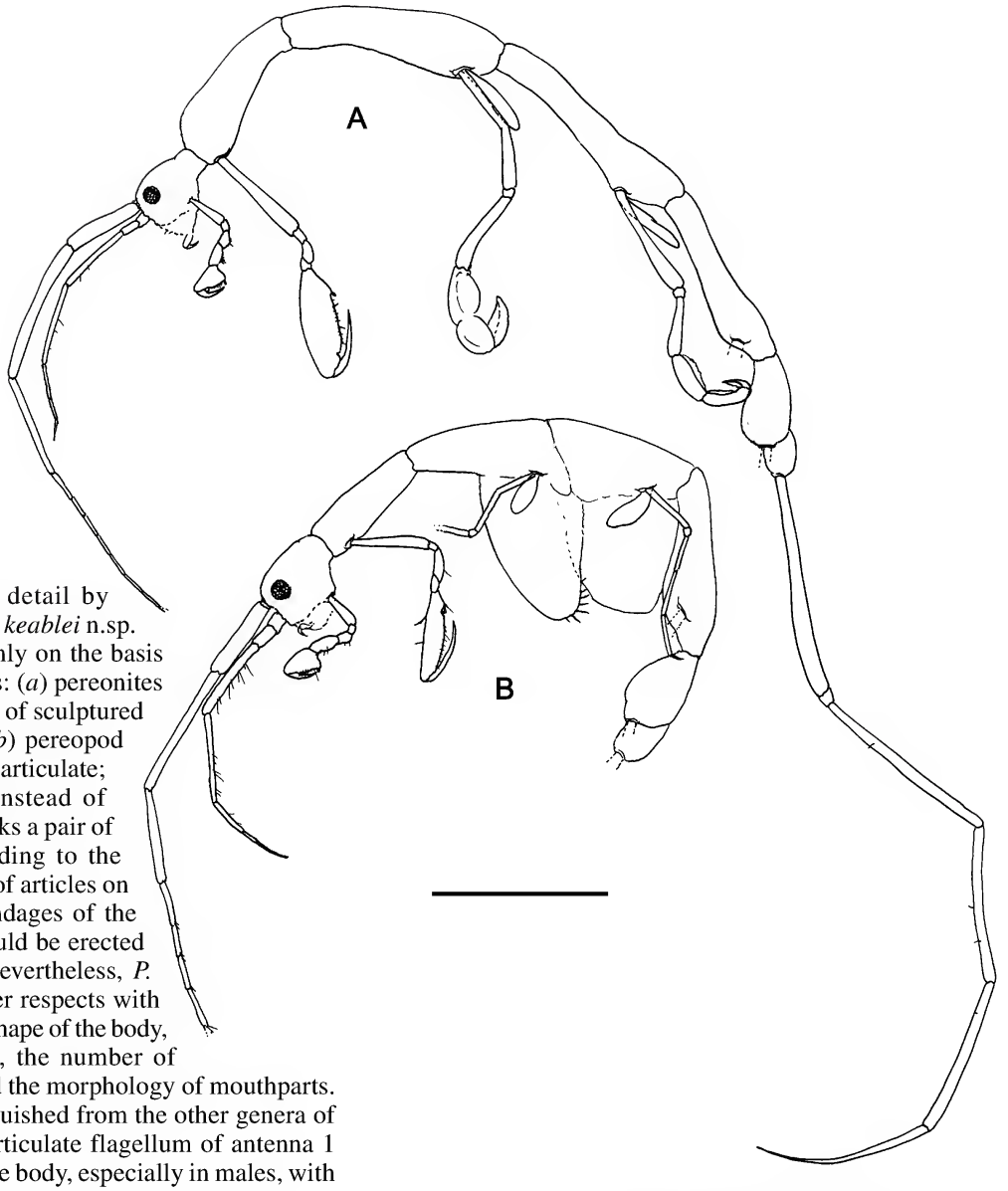


Fig. 28. *Protogeton inflatus* Mayer, 1903. Lateral view. (*A*) male; (*B*) female (ZMA Amph. 107194). Scale: 1 mm.

America, redescribed in detail by Laubitz (1970). *Perotripus keablei* n.sp. differs from *P. brevis* mainly on the basis of the following characters: (*a*) pereonites 2 and 3 are smooth instead of sculptured with lateral projections; (*b*) pereopod 3 uniarticulate instead of 3-articulate; (*c*) the penes are large instead of small; (*d*) the abdomen lacks a pair of small appendages. According to the differences in the number of articles on pereonite 3 and the appendages of the abdomen, a new genus could be erected for the present species. Nevertheless, *P. keablei* agrees well in other respects with *P. brevis*, as in the striking shape of the body, the structure of antennae, the number of articles on pereopod 5, and the morphology of mouthparts. • *Perotripus* can be distinguished from the other genera of the Phtisicinae by the 2-articulate flagellum of antenna 1 and the striking shape of the body, especially in males, with long pereonites 5 and 6.

Distribution. Presently known only from Lizard Island, Queensland, Australia.

Protogeton Mayer, 1903

Protogeton inflatus Mayer, 1903

Fig. 28

Protogeton inflatus Mayer, 1903: 28–29, pl. 1: fig. 13, pl. 6: figs. 29–32, pl. 9: figs. 11, 35, 51; Utinomi, 1947: 69.

Material examined. Syntypes, 1♂, 1♀, ZMA Amph. 107194, Dongala, Celebes (=Sulawesi) Indonesia; 1♂, QLD 1582 (poor condition); 2♂♂, 3♀♀, QM W12566, Middle Banks, Moreton Bay, Queensland, Australia, P. Saenger & J. Cook, 1983.

Remarks. *Protogeton* is characterized by the absence of abdominal appendages. Among phtisicines, this character is also present in *Pseudoproto* Mayer, 1903. Nevertheless, features of pereopods 3 and 4 in males of *Protogeton inflatus* are unique within the Caprellidae: the carpi, propodi and dactyli are curved, and with lateral expansions. Furthermore, the mandibular palp is reduced to one article in *Protogeton* while is normally 3-articulate in *Pseudoproto*. The specimens studied from Queensland are in agreement with the type material described by Mayer (1903) from Indonesia. Taking into consideration that material of *Protogeton inflatus* from Queensland was in poor condition, type material is illustrated to facilitate identification.

Distribution. Dongala, Celebes, Indonesia (Mayer, 1903), Tanabe Bay, Japan (McCain & Steinberg, 1970), Philippines and Papua New-Guinea (Guerra-García, 2002a, 2003); a new record for Australia.

Pseudoprellicana n.gen.

Diagnosis. Antenna 2 flagellum 2-articulate. Gills present on pereonites 3 and 4. Pereopods 3 and 4 absent. Pereopod 5 3-articulate. Pereopods 6 and 7 six-articulate. Mandibular palp 3-articulate. Molar absent. Abdomen with two pairs of appendages.

Etymology. The name is derived from "*Pseudo*" and "*Prellicana*" because the new genus strongly resembles *Prellicana*. Gender: feminine.

Type species. *Pseudoprellicana johnsoni* n.sp., by present designation and monotypy.

Remarks. The new genus is close to *Prellicana* Mayer, 1903. The main difference between these two genera is the presence of one pair of uniarticulate abdominal appendages in *Prellicana* and two pairs in *Pseudoprellicana*. In connection with the mouthparts, the inner plates of the maxilliped are partially fused in *Prellicana*, with three denticulate nodular setae, while in *Pseudoprellicana* the inner plates are not fused and instead of nodular setae the surface is transformed into a structure similar to a molar process. Pereopods 6 and 7 are similar in both genera but pereopod 5 is slightly different. Although in both genera the pereopod 5 is 3-articulate, in *Prellicana* the basal article is almost divided into two articles while it is not in *Pseudoprellicana*. The new genus is readily distinguished from *Jigurru* by the presence of two instead of three pairs of gills.

Pseudoprellicana johnsoni n.sp.

Figs 29–32

Type material. HOLOTYPE ♂, AM P61737, between Bird Islet & South Island, Lizard Island, Queensland, Australia, 14°40'S 145°, sediment at reef base with mixed algae, 25 m, GBR 27, J.K. Lowry, 9 Oct 1978. PARATYPES (all Lizard Island, Queensland): 1♀, AM P61738, between Bird Islet & South Island, 14°41'S 145°28'E, sediment at reef base with mixed algae, 25 m, GBR 29, J.K. Lowry, 9 Oct 1978; 1♀, AM P61739, between Bird Islet & South Island, 14°40'S 145°28'E sediment at reef base with mixed algae 25 m, GBR 28, P.C. Terrill, 9 Oct 1978.

Etymology. The species is dedicated to Rick Johnson, Australian Museum, for patiently registering all the material in the collections, and for his help and friendship during my stay at the Australian Museum.

Diagnosis. As for genus.

Description

Holotype male. • *Body length* 2.8 mm. • *Lateral view* (Fig. 29A). Body smooth without projections; head rounded; suture between head and pereonite 1 absent; pereonites 2–5 increasing in size respectively; pereonite 7 the shortest. • *Gills* (Fig. 29A) present on pereonites 3–4, oval, length about 2 times width.*Mouthparts*. Upper lip (Fig. 30B) symmetrically bilobed, lobes poorly demarcated, smooth apically. Mandibles (Fig. 30D,E) without molar; left mandible (Fig. 30D) with 5-toothed incisor and lacinia mobilis, followed by a row of plates decreasing in size; right mandible (Fig. 30E) with 5-toothed incisor, lacinia mobilis coarsely toothed, followed by row of plates decreasing in size; palp 3-articulate, second article with one seta, distal article with two setae. Lower lip (Fig. 30C) with inner lobes well demarcated; inner and outer lobes smooth, without setae. Maxilla 1 (Fig. 30F) outer lobe with six robust setae; distal article of palp with three robust setae and three serrate teeth distally and row of three setae laterally. Maxilla 2 (Fig. 30G) inner lobe oval with four setae; outer lobe rectangular, about 1.3 times longer than inner lobe, with five setae. Maxilliped (Fig. 30A) inner plate distally forming molar-like process with two setae; outer plate with three simple setae and serrate margin; palp four-articulate, dactylus smooth. • *Antennae*. Antenna 1 (Fig. 31A) about ⅓ of the body length; flagellum 3-articulate. Antenna 2 (Fig. 31B) almost half-length of antenna 1; swimming setae absent;

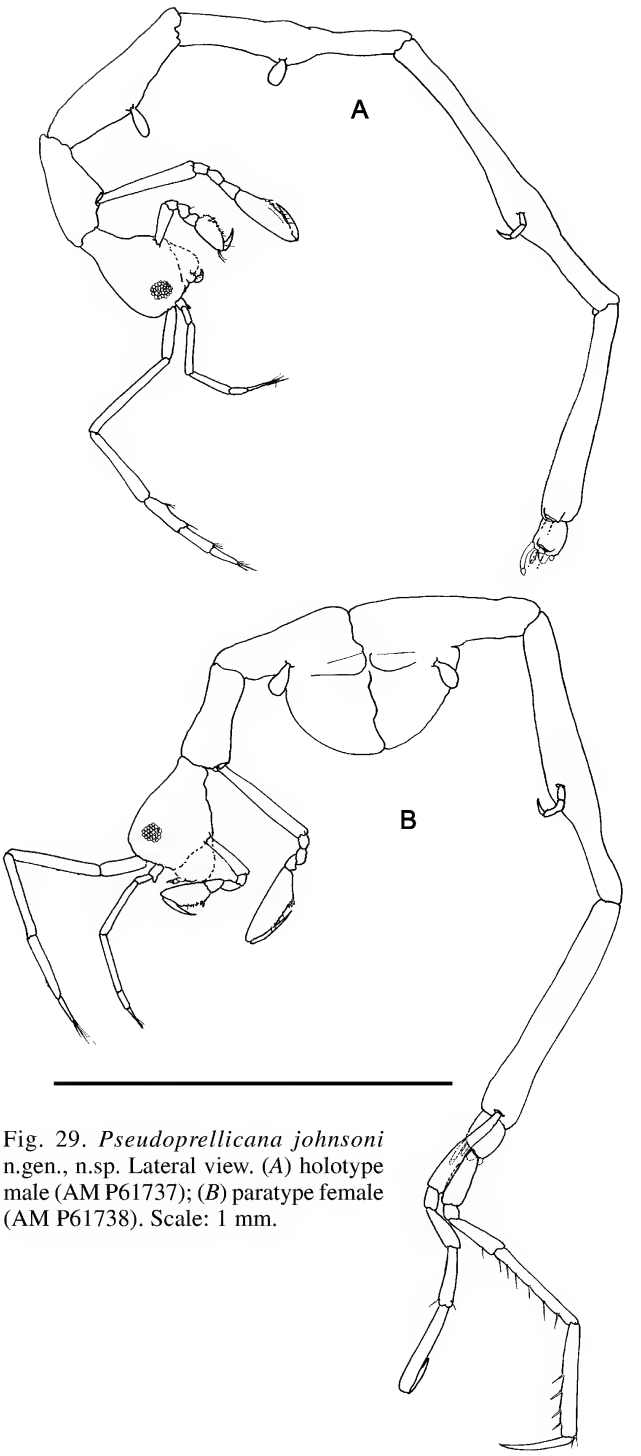


Fig. 29. *Pseudoprellicana johnsoni* n.gen., n.sp. Lateral view. (*A*) holotype male (AM P61737); (*B*) paratype female (AM P61738). Scale: 1 mm.

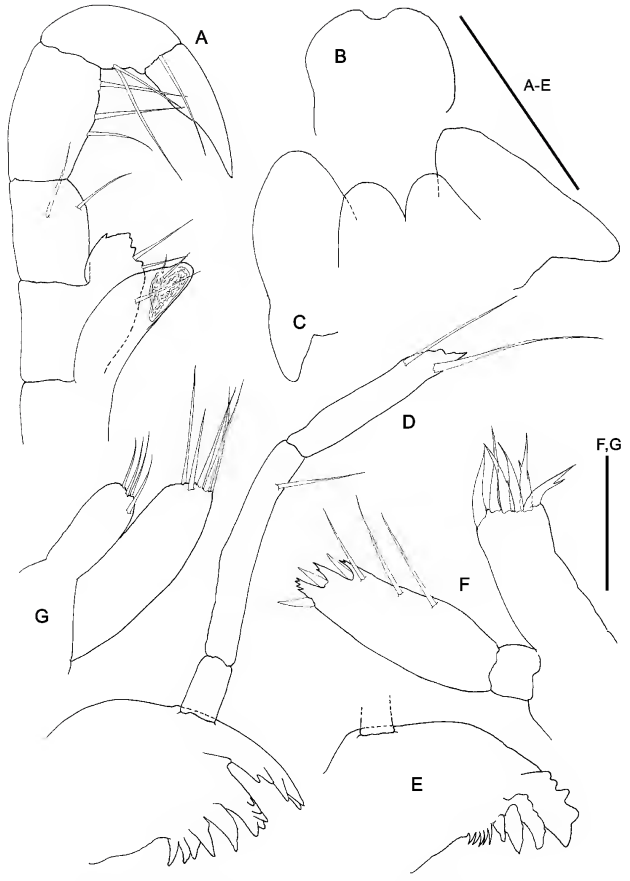


Fig. 30. *Pseudoprellicana johnsoni* n.gen., n.sp. Holotype male (AM P61737). (*A*) maxilliped; (*B*) upper lip; (*C*) lower lip; (*D*) left mandible; (*E*) right mandible; (*F*) maxilla 1; (*G*) maxilla 2. Scales 0.05 mm.

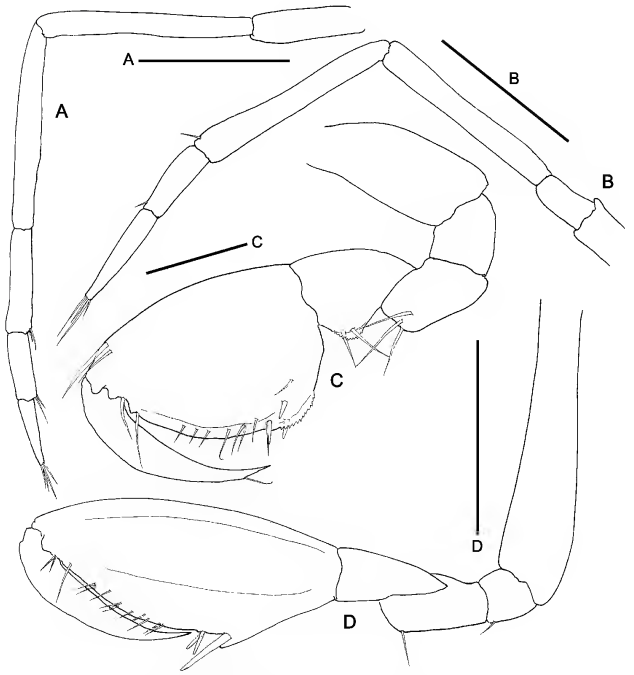


Fig. 31. *Pseudoprellicana johnsoni* n.gen., n.sp. Holotype male (AM P61737). (*A*) antenna 1; (*B*) antenna 2; (*C*) gnathopod 1; (*D*) gnathopod 2. Scales 0.1 mm.

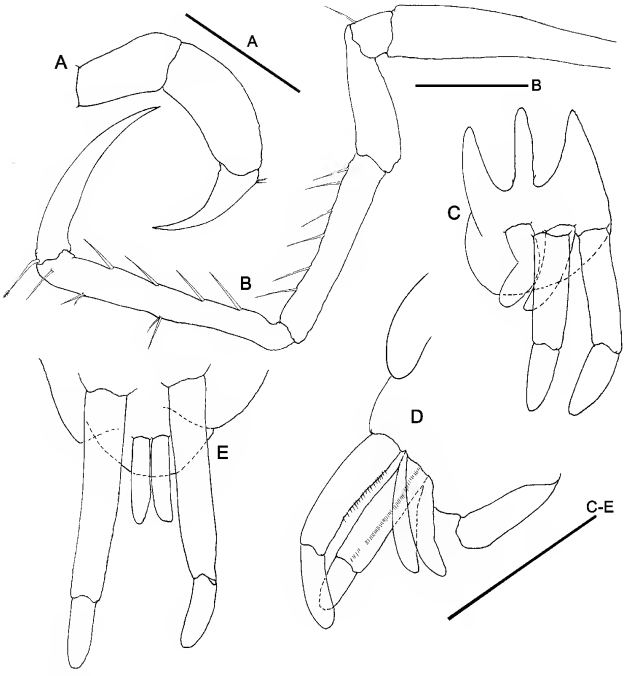


Fig. 32. *Pseudoprellicana johnsoni* n.gen., n.sp. (*A,C,D*) holotype male (AM P61737); (*B,E*) paratype female (AM P61738). (*A*) pereopod 5; (*B*) pereopod 7; (*C,E*) abdomen (ventral view); (*D*) abdomen (lateral view).

flagellum 2-articulate. • *Gnathopods*. Gnathopod 1 (Fig. 31C) basis as long as the ischium, merus and carpus combined; ischium and merus rectangular; carpus triangular with serrate margin ventrally; propodus oval, length about 1.5 times width, palm with three proximal grasping spines, grasping margin serrate on anterior half; dactylus slightly curved, with a distal seta. Gnathopod 2 (Fig. 31D) inserted on anterior part of pereonite 2; basis as long as pereonite 2; ischium rectangular; merus and carpus slightly elongate; propodus elongate (length about 2.5 times width), with three proximal grasping spines and row of setae along palm; dactylus short and slightly curved, smooth. • *Pereopods*. Pereopod 3 and 4 absent (Fig. 29A). Pereopod 5 3-articulate (Fig. 32A). Pereopods 6 and 7 missing (described from the female paratype AM P61738) • *Penes* (Fig. 32C,D) elongate, three times as long as wide with small apical suture. • *Abdomen* (Fig. 32C,D) with two pair of appendages and small dorsal lobe; first pair of appendages long, 2-articulate; second pair shorter, uniarticulate.

Paratype female. • *Body length* 2.7 mm. Oostegites (Fig. 29B) not setose. Gnathopods and abdomen (Fig. 32E) similar to those of holotype male. Pereopods 6 and 7 (Fig. 32B) subequal, six-articulate, carpus and propodus elongate, with row of setae ventrally; dactylus with plumose seta distally.

Remarks. Despite extensive sampling at Lizard Island, only three specimens of *Pseudoprellicana johnsoni* n.sp. were found, all on sediments at 25 m depth. Whether the species is naturally uncommon, or has narrow habitat requirements, remains to be determined.

Distribution. Presently known only from Lizard Island, Queensland.

Pseudoproto Mayer, 1903

Pseudoproto fallax Mayer, 1903

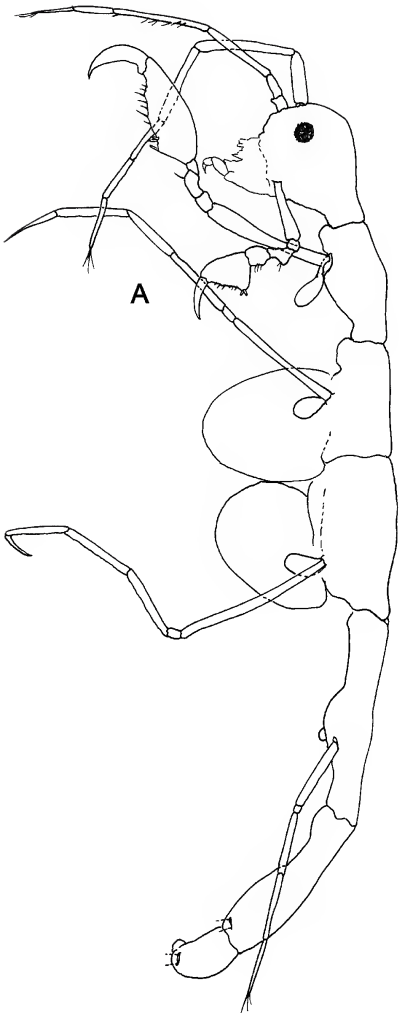
Fig. 33

Pseudoproto fallax Mayer, 1903: 27–28, pl. 6, fig. 22; pl. 9, figs 5, 52; Mayer, 1912: 8–9, fig. 3; Utinomi, 1947: 69.

Material examined. 4 syntype females, 1 syntype juvenile, ZMUC-CRU-6398, Koh Kauv and Koh Chuen, Thailand; 1 premature ♀, 1♀, AM P61734 (QLD 1475).

Remarks. Only two specimens of *P. fallax* were found during the present study, collected from filamentous algal turf attached to dead, thick, branching hard coral. Although no males were found, the present specimens are identified as *P. fallax* after consulting the type material of the species and on the basis of the combination of the following characters: three pairs of gills, flagellum of antenna 2 with two articles, pereopod 3 and 4 six-articulate, pereopod 5 five-articulate with the distal article elongate and provided with setae distally.

Distribution. Koh Kauv and Koh Chuen, Thailand (Mayer, 1903), Shark Bay, Western Australia (McCain & Steinberg, 1970); a new record for Queensland, Australia.



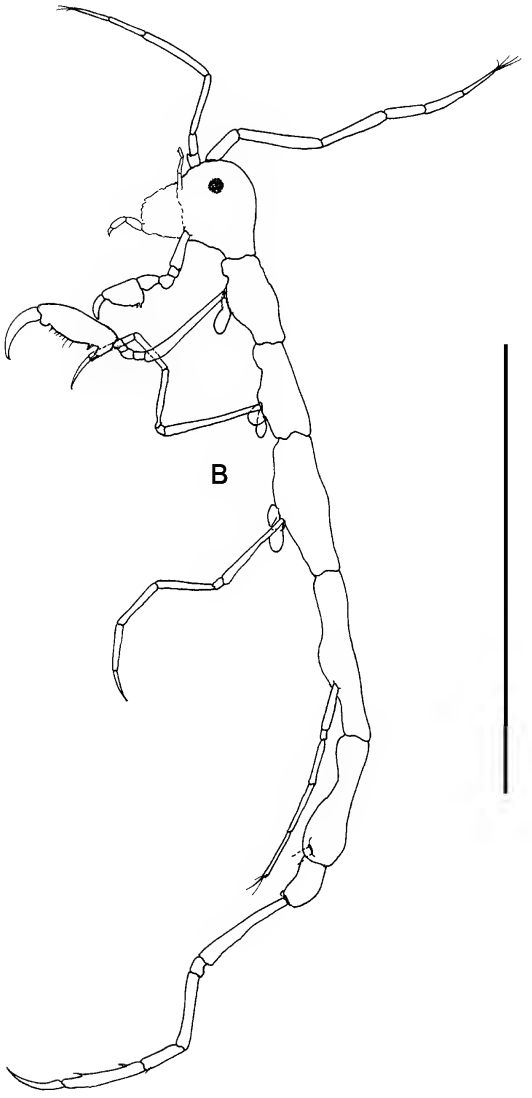


Fig. 33. *Pseudoproto fallax* Mayer, 1903. Lateral view. (*A*) female; (*B*) premature female. (AM P61734). Scale: 1 mm.

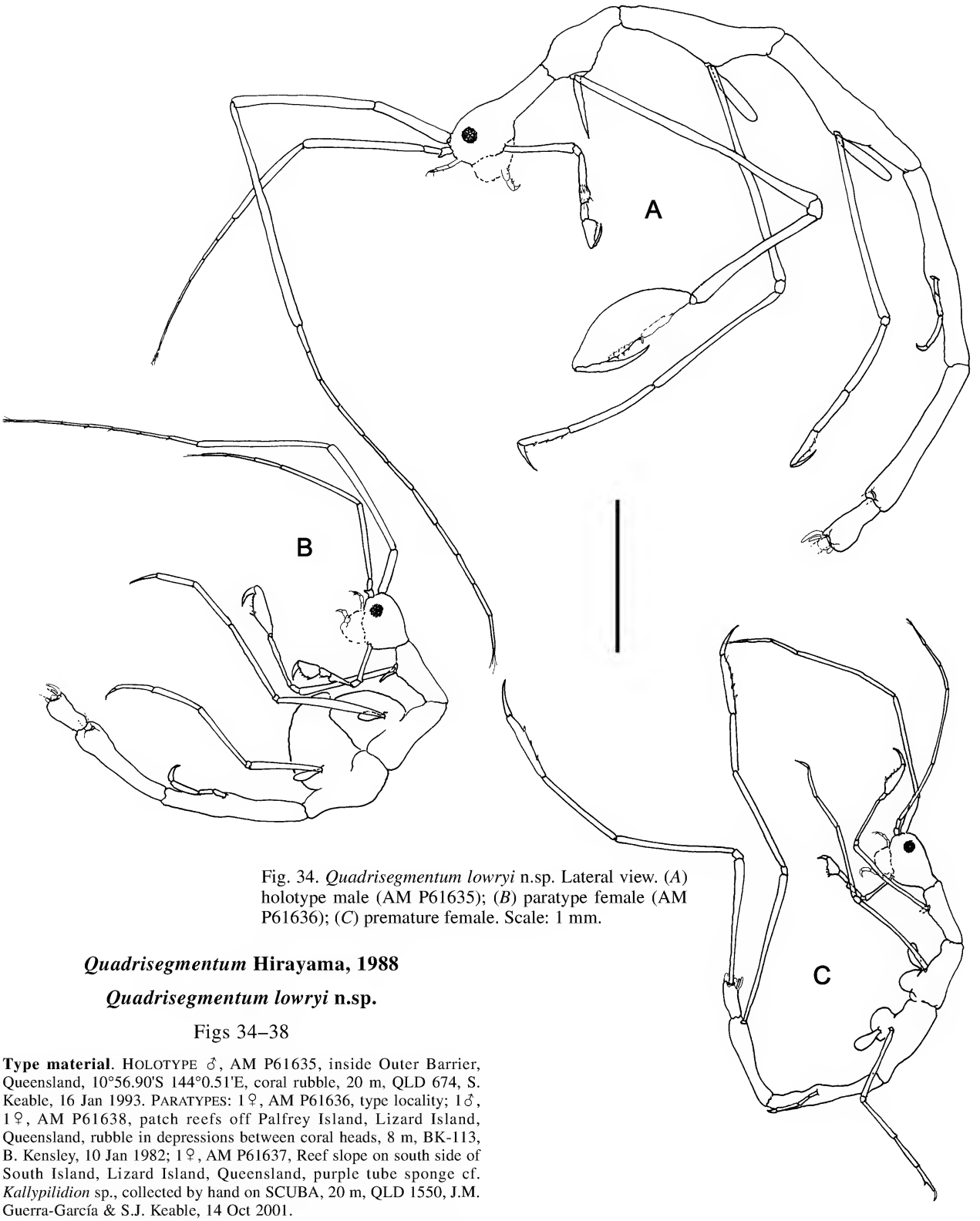


Fig. 34. *Quadrisegmentum lowryi* n.sp. Lateral view. (*A*) holotype male (AM P61635); (*B*) paratype female (AM P61636); (*C*) premature female. Scale: 1 mm.

Quadrisegmentum Hirayama, 1988

Quadrisegmentum lowryi n.sp.

Figs 34–38

Type material. HOLOTYPE ♂, AM P61635, inside Outer Barrier, Queensland, 10°56.90'S 144°0.51'E, coral rubble, 20 m, QLD 674, S. Keable, 16 Jan 1993. PARATYPES: 1♀, AM P61636, type locality; 1♂, 1♀, AM P61638, patch reefs off Palfrey Island, Lizard Island, Queensland, rubble in depressions between coral heads, 8 m, BK-113, B. Kensley, 10 Jan 1982; 1♀, AM P61637, Reef slope on south side of South Island, Lizard Island, Queensland, purple tube sponge cf. *Kallypilidion* sp., collected by hand on SCUBA, 20 m, QLD 1550, J.M. Guerra-García & S.J. Keable, 14 Oct 2001.

Etymology. Named after Jim Lowry, Australian Museum for his help and hospitality during my stay at the Australian Museum, and for his considerable contributions to the knowledge of the amphipod crustaceans along the world.

Diagnosis. Body dorsally smooth. Gills on pereonites 2–4. Pereopods 3 and 4 longer than pereonites 3 and 4 combined. Propodus of male gnathopod 2 without projection. Abdominal appendages uniarticulate.

Description

Holotype male. • *Body length*. 6.2 mm. • *Lateral view* (Fig. 34A). Body smooth dorsally. Head rounded. Pereonite 1 fused with head, suture absent; pereonites 2–5 increasing slightly in length respectively; pereonite 7 the shortest. • *Gills* (Fig. 34A). Present on pereonites 2–4. Elongate, length about 4 times width. First pair, on pereonite 2,

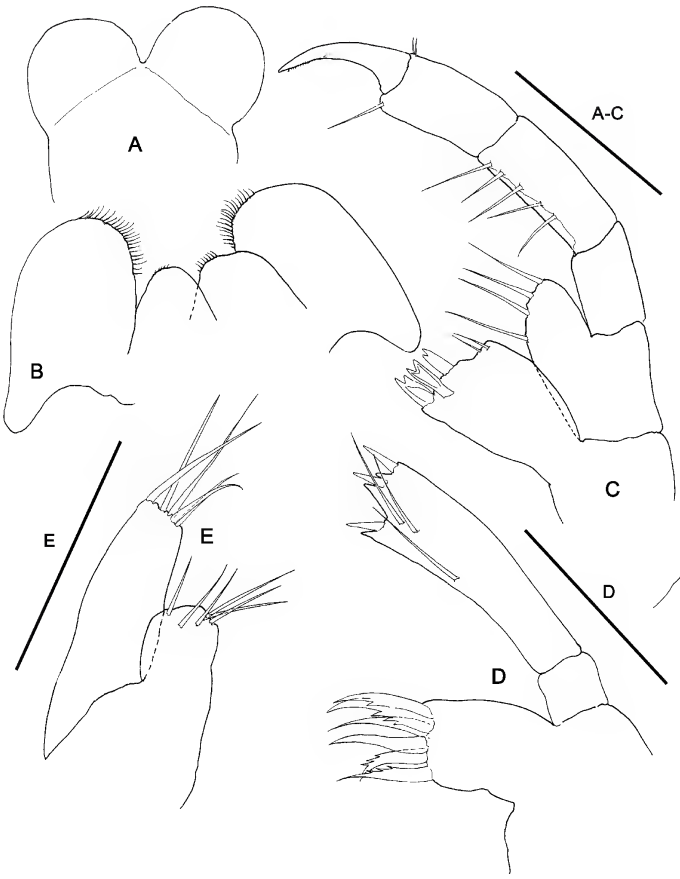


Fig. 35. *Quadrisegmentum lowryi* n.sp. Holotype male (AM P61635). (*A*) upper lip; (*B*) lower lip; (*C*) maxilliped; (*D*) maxilla 1; (*E*) maxilla 2. Scales 0.05 mm.

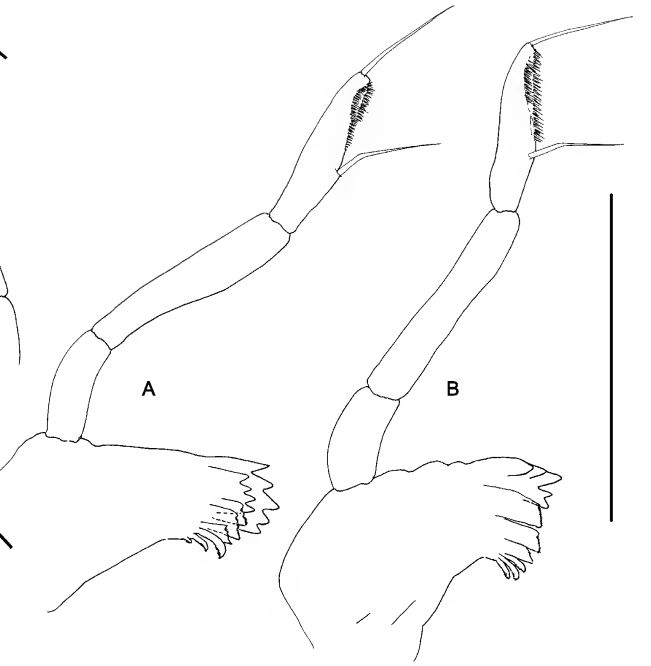


Fig. 36. *Quadrisegmentum lowryi* n.sp. Holotype male (AM P61635). (*A*) left mandible; (*B*) right mandible mandible. Scale: 0.1 mm.

triangular. • *Mouthparts*. Upper lip (Fig. 35A) symmetrically bilobed, lobes well demarcated and smooth apically. Mandibles (Fig. 36A,B) with 3-articulate palp; distal article of palp with two setae and two rows of minute setulae; mandibular molar absent; left mandible (Fig. 36A) with incisor 5-toothed, lacinia mobilis 4-toothed followed by three plates and three plumose setae; incisor of right mandible (Fig. 36B) 5-toothed, lacinia mobilis forming minutely serrate plate, followed by two more plates and three plumose setae; molar flake absent. Lower lip (Fig. 35B) with inner lobes well-demarcated; inner and outer lobes provided with setulae on apical end. Maxilla 1 (Fig. 35D) outer lobe with six robust setae serrate; distal article of palp with three robust setae and three teeth distally, and three setae medially. Maxilla 2 (Fig. 35E) inner lobe oval, with six setae distally; outer lobe elongate, rectangular, 1.5 times as long as inner lobe, with five apical setae. Maxilliped (Fig. 35C) inner plate with three robust nodular setae (like teeth) distally; outer plate smaller than inner plate with four setae; palp four-articulate, articles 1–3 rectangular, article 4 (dactylus) small and curved. • *Antennae*. Antenna 1 (Fig. 37A) almost as long as the body; flagellum 11-articulate; peduncular articles elongate. Antenna 2 (Fig. 37B) flagellum six-articulate; proximal article of peduncle with small projection distally; articles 3 and 4 of peduncle elongate; swimming setae absent. • *Gnathopods*. Gnathopod 1 (Fig. 37C) basis as long as ischium, merus and carpus combined; ischium short and rectangular; merus with setulae and four setae on distal end; propodus triangular, palm with four proximal grasping spines; dactylus smooth and scarcely curved. Gnathopod 2 (Fig. 37D) inserted on anterior half of pereonite 2; basis about three times as long as pereonite 2; ischium rectangular; merus elongate, about the half basis length; carpus short and triangular; propodus as long as merus; palm with proximal cavity filled with a membranous sack, followed by a grasping spine and two distal rows of smaller spines along the palm; dactylus smooth, strongly curved. • *Pereopods*. Pereopods 3 (Fig. 38A) and 4 (Fig. 38B) six-articulate. Propodus with three grasping spines along palm on pereopod 3 and four spines on pereopod 4; merus and carpus longer on pereopod 3 than on pereopod 4. Pereopod 5 (Fig. 38C) four-articulate. Pereopods 6 and

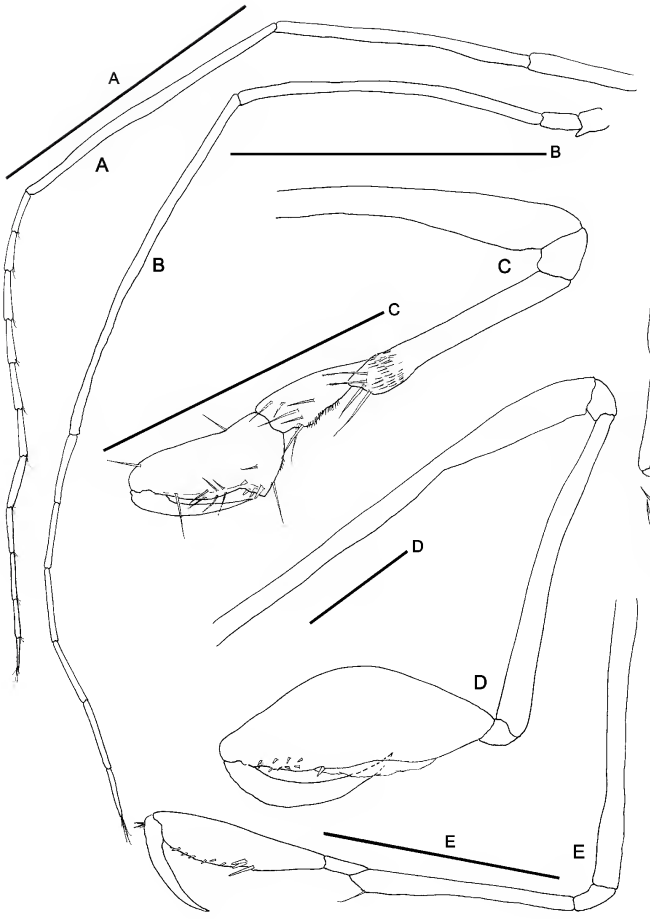


Fig. 37. *Quadrisegmentum lowryi* n.sp. (*A–D*) holotype male (AM P61635). (*A*) antenna 1; (*B*) antenna 2; (*C*) gnathopod 1; (*D*) gnathopod 2; (*E*) paratype female (AM P61636) gnathopod 2. Scales: A: 0.5 mm; B: 0.1 mm; C: 0.3 mm; D,E: 0.2 mm.

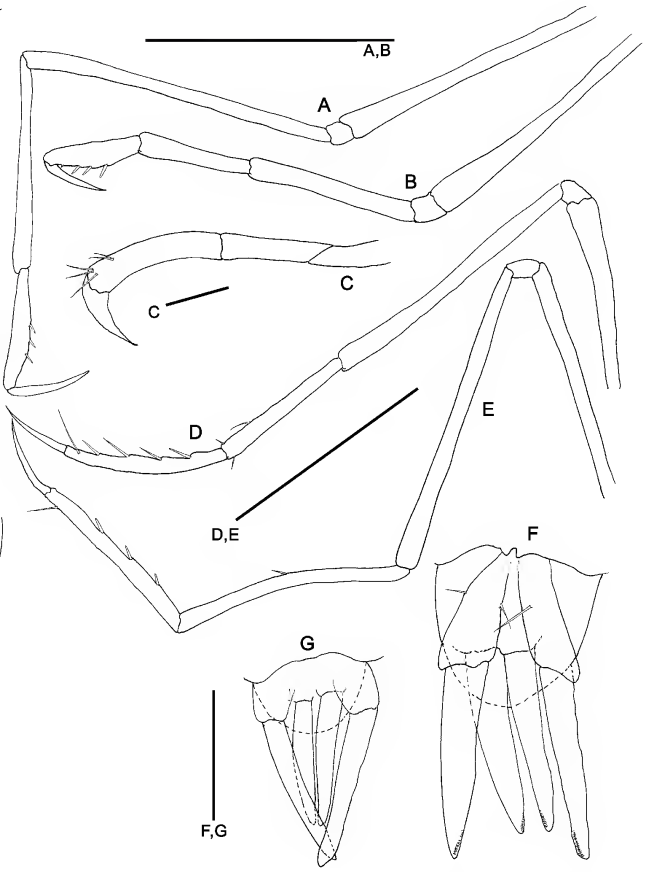


Fig. 38. *Quadrisegmentum lowryi* n.sp. (*A–C,F*) male holotype (AM P61635); (*D,E,G*) paratype female. (*A*) pereopod 3; (*B*) pereopod 4; (*C*) pereopod 5; (*D*) female pereopod 6; (*E*) female pereopod 7; (*F*) G, abdomen (ventral view). Scales: A,B,D,E: 0.5 mm; C: 0.1 mm; F,G: 0.05 mm.

7 missing in holotype (described for female below). • *Penes*. Reduced to a pair of tiny appendages situated medially (Fig. 38F). • *Abdomen*. (Fig. 38F) with two pair of uniarticulate appendages (although the first pair is provided with a basal peduncle), and a dorsal lobe.

Paratype female. • *Body length* 3.8 mm. Flagellum of antenna 1 seven-articulate; flagellum of antenna 2 3-articulate (Fig. 34B). Carpus of gnathopod 2 (Fig. 37E) about three times as long as wide, more elongate than in male, with 3 grasping spines and without membranous sack proximally. Pereopods 6 and 7 (Fig. 38D,E, 34C) six-articulate, propodus with four grasping spines and one setae on pereopod 6 and three grasping spines and one setae on pereopod 7. Oostegites not setose (Fig. 34B).

Remarks. *Quadrisegmentum lowryi* n.sp is close to its only congener *Q. triangulum*. The main differences between the two species are: (*a*) the antennae, gnathopods and pereopods 6 and 7 are clearly longer in *Q. lowryi*; (*b*) the propodus of the gnathopod 2 male is provided with a developed distal triangular projection in *Q. triangulum* while this projection is absent in *Q. lowryi*; (*c*) the abdominal appendages are 2-articulate in *Q. triangulum* and one-articulate in *Q. lowryi*.

Besides these differences, the membranous sack present on the male propodus palm of *Q. lowryi* seems not to be present in *Q. triangulum* (Hirayama, 1988). Nevertheless this character should be used carefully because it varies allometrically. For example, Krapp-Schickel (1993) figured the variation of the gnathopod 2 in adult males of *Phtisica marina*. Some males of *Phtisica marina* (superadult) bear the membranous sac and one grasping spine, while another lacks the membranous structure, having 3 grasping spines proximally.

Distribution. Inside Outer Barrier (10°56.90'S 144°1.22'E) and Lizard Island, Queensland, Australia.

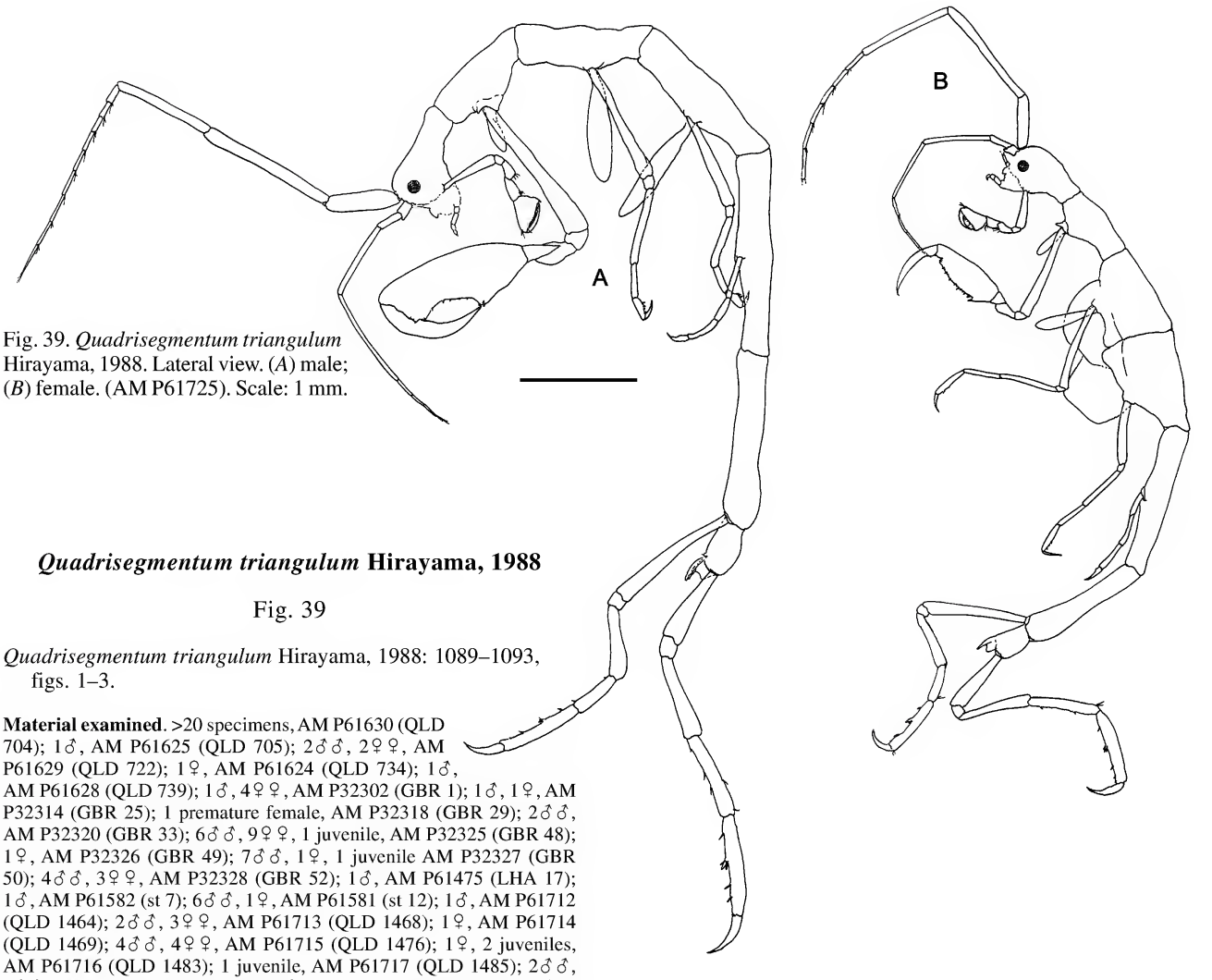


Fig. 39. *Quadrisegmentum triangulum* Hirayama, 1988. Lateral view. (*A*) male; (*B*) female. (AM P61725). Scale: 1 mm.

Quadrisegmentum triangulum Hirayama, 1988

Fig. 39

Quadrisegmentum triangulum Hirayama, 1988: 1089–1093, figs. 1–3.

Material examined. >20 specimens, AM P61630 (QLD 704); 1♂, AM P61625 (QLD 705); 2♂♂, 2♀♀, AM P61629 (QLD 722); 1♀, AM P61624 (QLD 734); 1♂, AM P61628 (QLD 739); 1♂, 4♀♀, AM P32302 (GBR 1); 1♂, 1♀, AM P32314 (GBR 25); 1 premature female, AM P32318 (GBR 29); 2♂♂, AM P32320 (GBR 33); 6♂♂, 9♀♀, 1 juvenile, AM P32325 (GBR 48); 1♀, AM P32326 (GBR 49); 7♂♂, 1♀, 1 juvenile AM P32327 (GBR 50); 4♂♂, 3♀♀, AM P32328 (GBR 52); 1♂, AM P61475 (LHA 17); 1♂, AM P61582 (st 7); 6♂♂, 1♀, AM P61581 (st 12); 1♂, AM P61712 (QLD 1464); 2♂♂, 3♀♀, AM P61713 (QLD 1468); 1♀, AM P61714 (QLD 1469); 4♂♂, 4♀♀, AM P61715 (QLD 1476); 1♀, 2 juveniles, AM P61716 (QLD 1483); 1 juvenile, AM P61717 (QLD 1485); 2♂♂, 3♀♀, AM P61718 (QLD 1524); 1♀, AM P61719 (QLD 1526); 1♂, 1 premature female, AM P61720 (QLD 1528); 2♀♀, AM P61721 (QLD 1536); 1♂, AM P61722 (QLD 1541); >20 specimens, AM P61723 (QLD 1544); 1♂, AM P61724 (QLD 1545); 2♂♂, AM P61725 (QLD 1565); 1♀, AM P61726 (QLD 1568); 1♀, AM P61727 (QLD 1569); 1♂, 1 juvenile, AM P61728 (QLD 1573); 1♂, AM P61729 (QLD 1581); 1♂, AM P61730 (QLD 1588).

Remarks. *Quadrisegmentum* was recently established by Hirayama (1988) for *Q. triangulum*. The material examined from Queensland agrees well with the specimens described by Hirayama (1988). This is one of the most abundant caprellid species on the Great Barrier Reef.

Distribution. West Islet, Ashmore Reef, Northwest Australia (12°14.28'S 122°59.14'E) (Hirayama, 1988), Papua New Guinea (Guerra-García, 2003); a new record for Queensland, Australia.

Subfamily Caprellinae Leach, 1814

Aciconula Mayer, 1903

Aciconula australiensis Guerra-García, 2004

Fig. 40

Aciconula australiensis Guerra-García, 2004: 23–29, figs. 19–23.

Material examined. 1 ♂, AM P61735 (QLD 1475); 1 ♀, 1 juvenile, AM P61736 (QLD 1567).

Remarks. This species is uncommon on the Great Barrier Reef. Only three specimens were collected from Lizard Island, clinging to small hydroids or algal turf on dead corals. *Aciconula australiensis* was recently described based on specimens collected from Western Australia (Guerra-García, 2004). The specimens from Queensland are indistinguishable from Western Australian specimens, apart from minor differences in body ornamentation that can be attributed to differences in development.

Distribution. Dampier Archipelago, Western Australia, and now from Queensland, Australia.

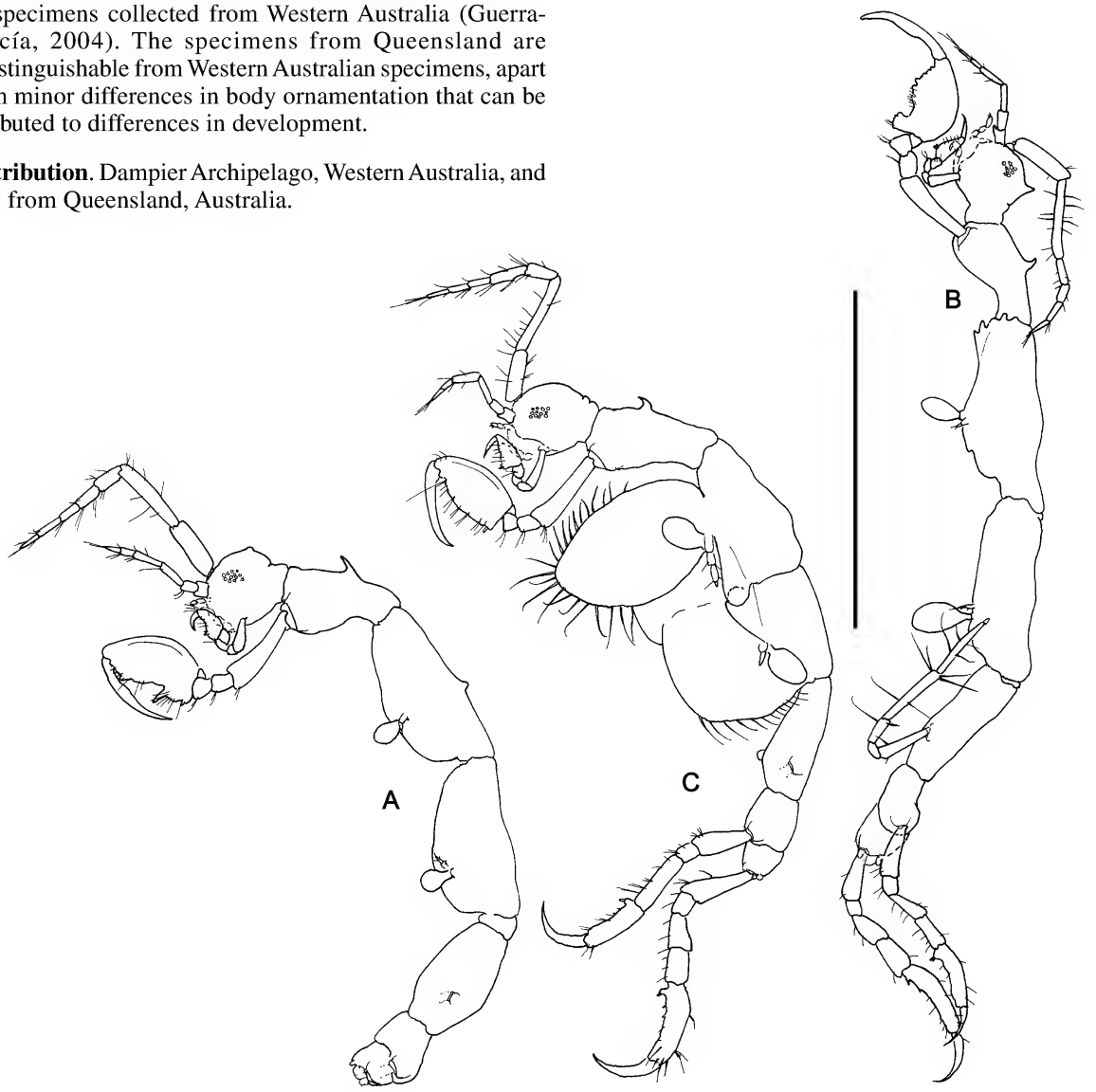


Fig. 40. *Aciconula australiensis* Guerra-García, 2004. Lateral view. (*A,B*) males; (*C*) female. Refigured from Guerra-García (2004). Scale: 1 mm.

Caprella Lamarck, 1801

Caprella danilevskii Czerniavskii, 1868

Fig. 41

Caprella Danilevskii Czerniavskii, 1868: 92, pl. 6: figs. 21–34; Mayer, 1890: 58, pl. 5: fig. 44; pl. 7: figs. 12–13.
Caprella Danilewskii Chevreux & Fage, 1925: 454, fig. 432.
Caprella danilevskii McCain, 1968: 22, figs. 10–11; McCain & Steinberg, 1970: 16; Cavedini, 1982: 499; Krapp-Schickel, 1993: 779, fig. 531; Guerra-García & Takeuchi, 2002: 683–684, fig. 6.
Caprella inermis Haswell, 1879: 319–351.

Material examined. 1♂, 1 premature female, AM P61639 (QLD 949); 1♂, 2 female, AM P61640 (QLD 954); 1♂, AM P61641 (QLD 957); 3 female, AM P61642 (QLD 968); 1♂, AM P61643 (QLD 969); 2 male, AM P61644 (QLD 972); 1♂, AM P61645 (QLD 979); 3♂♂, 2♀♀, AM P61476 (LHA 48); 2♂♂, 3♀♀, AM P61477 (LHA 49); 1♀, AM P61478 (LHA 51); 1♂, AM P43062, Bustard Head, south of Gladstone, Queensland, 24°02'S 151°46'E, among *Sargassum* on rocks, J.S. Hynd, 28 Aug 1946; >20 specimens, AM P61334, Miami, Queensland, 28°04'S 153°27'E, among weed on rocky headland, J.S. Hynd, Aug 1944.

Remarks. *Caprella danilevskii* is a cosmopolitan species (Krapp-Schickel, 1993). The distinctive male abdomen, the absence of grasping spines on the pereopods and the short dactylus of male gnathopod 2 distinguish this species from other species of *Caprella*. The morphology of Queensland specimens agrees with published accounts (Krapp-Schickel, 1993; Guerra-García & Takeuchi, 2002). The species has been found mainly in southern Queensland, around Shoalwater Bay, Lord Howe Island and the coast near Brisbane. Apparently, this species favours no-coralline habitats.

Distribution. Cosmopolitan (Krapp-Schickel, 1993); a new record for Queensland.

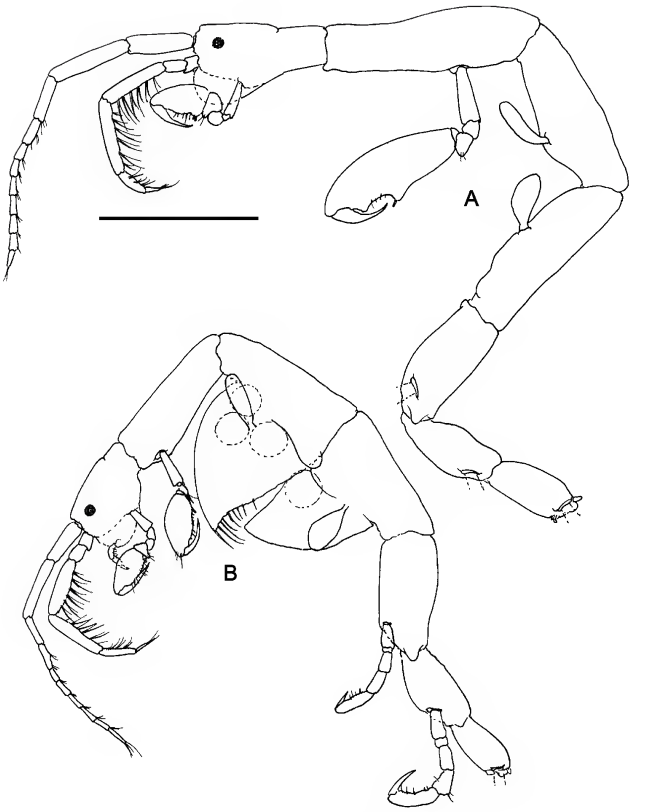


Fig. 41. *Caprella danilevskii* Czerniavskii, 1868. Lateral view. (*A*) male (AM P61476); (*B*) female (AM P61477). Scale: 1 mm.

Caprella penantis Leach, 1814

Fig. 42

Caprella Penantis Leach, 1814: 404.
Caprella acutifrons Mayer, 1882: 48; Mayer, 1890: 50, pl. 2: figs. 36–37, 39–41, pl. 4: figs. 52–53, 55, 57–61, 65–69; Mayer, 1903: 79, pl. 3: figs. 4–28; pl. 7: figs. 62–65.
Caprella penantis McCain, 1968: 33, figs.15–16; McCain & Steinberg, 1970: 33; Cavedini, 1982: 508; Krapp-Schickel, 1993: 791–793; Guerra-García & Takeuchi, 2002: 692–693, fig. 12.

Material examined. 4♂♂, 1 premature female, 3♀♀, 1 juvenile, AM P61632 (QLD 658); 1♂, 1 premature female, 1♀, 1 juvenile, AM P61631 (QLD 659).

Remarks. Although this species is believed to be cosmopolitan (Krapp-Schickel, 1993), its presence is only occasional along the Great Barrier Reef, having been found in only two samples to the north of the study area. *Caprella penantis* has been recorded under several species or subspecies names from temperate regions worldwide (McCain, 1968; Laubitz, 1972; Takeuchi & Hirano, 1995). Further studies are required to determine the status of these nominal taxa.

Distribution. Cosmopolitan; a new record for Queensland.

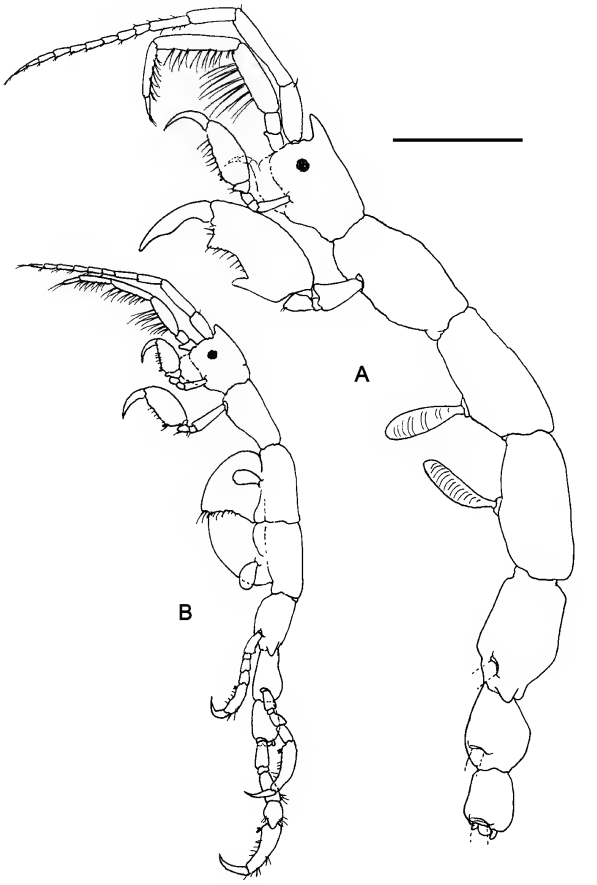


Fig. 42. *Caprella penantis* Leach, 1814. Lateral view. (*A*) male; (*B*) female. (AM P61632). Scale: 1 mm.

Hemiaegina Mayer, 1890

Hemiaegina minuta Mayer, 1890

Fig. 43

Hemiaegina minuta Mayer, 1890: 40, pl. 1: figs. 25–27, pl. 3: figs. 32–35, pl. 5: figs. 52–53, pl. 6: figs. 13, 33–34, pl. 7: fig. 4; McCain, 1968: 61–64, figs. 29–30; McCain & Steinberg, 1970: 51; Gable & Lazo-Wasem, 1987: 637; Müller, 1990: 836; Serejo, 1997: 630–632, fig. 1.
Hemiaegina quadripunctata Sundara Raj, 1927: 126–127, pl. 18.
Hemiaegina costai Quitete, 1972: 165–168, pls. 1–2.

Material examined. 1♂, AM P61647 (QLD 980); 5♂♂, 2♀♀, AM P61648 (QLD 979); 1♂, AM P61649 (QLD 972); 1♀, AM P61650 (QLD 957); 2♂♂, 3♀♀, AM P61651 (QLD 955); 1♂, AM P61652 (QLD 969); 1♀, AM P61815 (QLD 856); 1♂, 3♀♀, AM P61587 (st 30); 1♂, 1♀, AM P61588 (st 36); 2♂♂, 1♀, AM P61589 (st 43); 3♂♂, AM P61590 (st 45); 1♂, AM P61591 (st 1); 1♂, AM P61592 (st 7); 1♂, 1♀, AM P61593 (st 20); 1♂, AM P61594 (st 23); 2♂♂, 3♀♀, AM P61595 (st 21); 1♂, 1♀, AM P61474 (LHA 11); 1♂, AM P32307 (GBR 11); 1♂, 1♀, AM P61733 (BK-114); 1♂, QLD 1564.

Remarks. *Hemiaegina minuta* is widely distributed in tropical and temperate waters worldwide (Müller, 1990). The Queensland specimens agree with the description of McCain (1968) based on material from the West coast of North America.

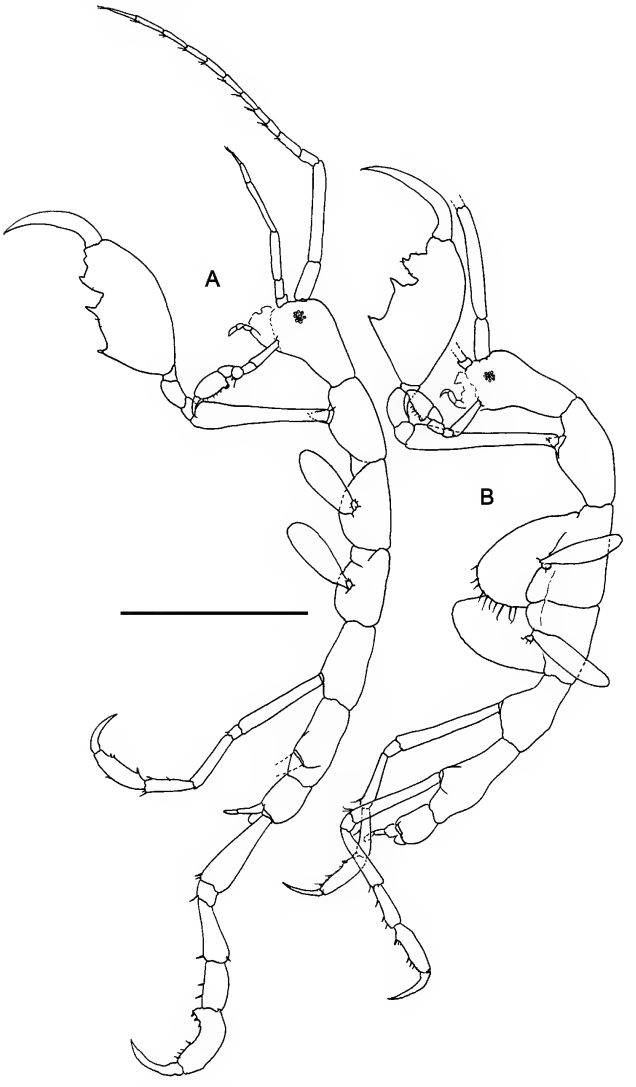


Fig. 43. *Hemiaegina minuta* Mayer, 1890. Lateral view. (*A*) male; (*B*) female. (AM P61648). Scale: 1 mm.

Distribution. Off Amoy, China, 15–46 m deep (Mayer, 1890); off Bermuda; Virginia; Cape Hatteras, North Carolina; Elliot Key, Florida; Loggerhead Key, Tortugas; 29°44'N 88°23.5'W; Port Aransas, Texas; St. John, Virgin Islands; False Bay, South Africa; Oahu, Hawaii; Bora Bora; Sunohama and Tateyama, Japan; 1°42.5'S 130°47.5'E; Fremantle, Australia; Krusadai Island, India; South Arabian coast (McCain & Steinberg, 1970); Papua New Guinea (Guerra-García, 2003); a new record for Queensland, Australia.

Metaprotella Mayer, 1890

Metaprotella sandalensis Mayer, 1898

Fig. 44

Metaprotella sandalensis Mayer, 1898: 53–56, figs. 1–6; Mayer, 1903: 40–42, pl. 1: figs. 30–31, 34–36, pl. 6: figs. 56–63, pl. 9: figs.16–17, 44, 60; Müller, 1990: 836–842, figs. 41–64; Müller, 1990: 836–842, figs. 41–64; Laubitz, 1991: 113, fig. 10.

Material examined. Four specimens in poor condition, AM P7986, Ellison Reef, Queensland, 17°43'S 146°25'E, from coral, 16 m. deep, W.E.G. Paradice, 1924; 1♂, AM P61670 (QLD 639); 4♂♂, 5♀♀, 6 juveniles, AM P61666 (QLD 650); >20 specimens, AM P61667 (QLD 646); 1 juvenile, AM P61668 (QLD 651); >20 specimens, AM P61673 (QLD 658); 4♂♂, 1 premature female, 1♀, 1 juvenile, AM P61665 (QLD 659); 1♂, 1 premature female, 4 female, 1 juvenile, AM P61672 (QLD 660); 1♂, 1♀, 4 juveniles, AM P61661 (QLD 664); 1♂, 1 premature female, 2 juveniles, AM P61662 (QLD 667); 1 juvenile, AM P61663 (QLD 668); 1♂, 1♀, 1 juvenile, AM P61669 (QLD 682); 1♂, 4 premature females, 8♀♀, AM P61671 (QLD 696); >20 specimens, AM P61687 (QLD 721); 1♀, AM P61680 (QLD 723); 1 premature female, AM P61679 (QLD 724); 1♂, AM P61685 (QLD 733);

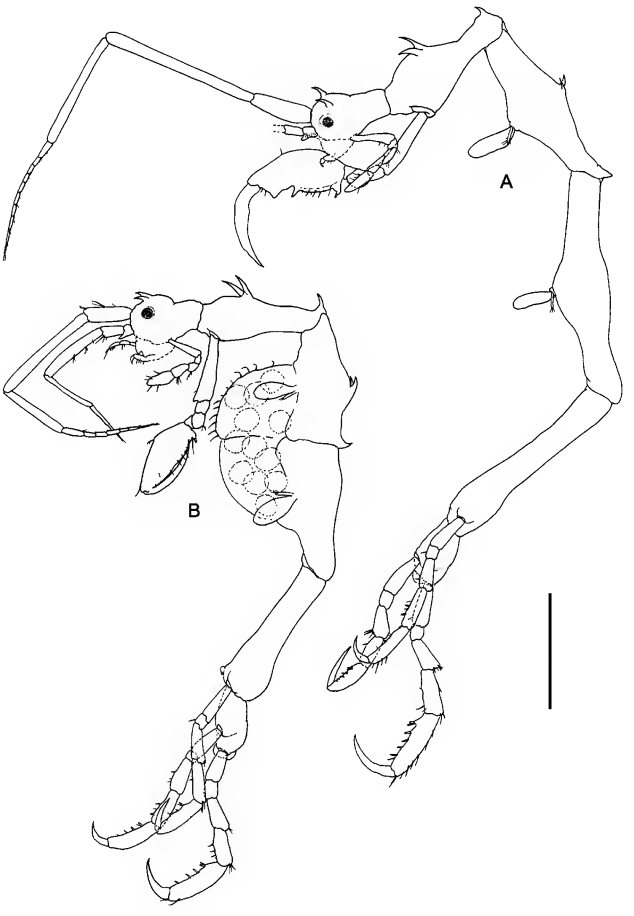


Fig. 44. *Metaprotella sandalensis* Mayer, 1898. Lateral view. (*A*) male; (*B*) female. (AM P61804). Scale: 1 mm.

1♂, AM P61681 (QLD 734); 3♀♀, AM P61684 (QLD 735); 1♂, 1♀, AM P61683 (QLD 760); 1 premature female, AM P61686 (QLD 777); 2♂♂, 1 premature female, AM P61682 (QLD 778); 2♂♂, 1 juvenile, AM P61658 (QLD 955); 1♂, AM P61657 (QLD 957); 6♂♂, 1 premature female, 3♀♀, AM P61656 (QLD 979); 3♂♂, 4♀♀, 2 juveniles, AM P61654 (QLD 983); 1 premature female, AM P61659 (QLD 985); 2♂♂, 1 premature female, 1♀, AM P61660 (QLD 986); 1♀, AM P61655 (QLD 990); 2♂♂, 2♀♀, AM P32306 (GBR 11); 5♂♂, 2♀♀, AM P32308 (GBR 12); 1♂, 1 premature female, 1♀, AM P32311 (GBR 19); 9♂♂, 3 premature females, 5♀♀, AM P32312 (GBR 20); 1♂, 1♀, AM P32313 (GBR 21); 2♂♂, 1 premature female, AM P32316 (GBR 27); 3 premature females, AM P32317 (GBR 28); 1♂, AM P61760, (GBR 29); 1♀, AM P32319 (GBR 30); 1♂, 2♀♀, AM P32322 (GBR 44); 2♂♂, 1♀, AM P32323 (GBR 45); 17♂♂, 6♀♀, 2 juveniles, AM P61761 (GBR 50); 1♂, 1 premature female, 4 juveniles, AM P32329 (GBR 55); 2♀♀, AM P32331 (GBR 59); 7♂♂, 1 premature female, 2♀♀, 4 juveniles, AM P61606 (st 1); 2 female, 2 juvenile, AM P61605 (st 8.1); 1♀, AM P61603 (st 10); 3♂♂, AM P61604 (st 14); 10♂♂, 3 premature females, 3♀♀, 12 juveniles, AM P61596, (st 30); 2♂♂, 1♀, AM P61597 (st 32); 2♂♂, 1♀, AM P61598 (st 34); 2♂♂, AM P61600 (st 36); 1♂, AM P61599 (st 37); 1♀, AM P61601 (st 38); 7♂♂, 2♀♀, 18 juveniles, AM P61602 (st 43); 1♀, AM P61779 (QLD 1464); 5♂♂, AM P61780 (QLD 1465); 2♂♂, 2♀♀, 2 juveniles, AM P61781 (QLD 1468); >20 specimens, AM P61782 (QLD 1470); 1♀, 1 juvenile, AM P61783 (QLD 1472); 2♂♂, 4♀♀, AM P61784 (QLD 1473); 3♂♂, AM P61785 (QLD 1474); 1♂, 1♀, AM P61786 (QLD 1476); 1 premature female, 1♀, AM P61787 (QLD 1477); >20 specimens, AM P61788 (QLD1478); >20 specimens, AM P61789 (QLD 1484); 1 juvenile, AM P61790 (QLD 1487); 1♂, AM P61791 (QLD 1488); 1♀, AM P61792 (QLD 1503); 1♂, AM P61793 (QLD 1509); 1♀, AM P61794 (QLD 1514); 4♂♂, 2♀♀, AM P61795 (QLD 1515); 6♂♂, 6♀♀, AM P61796 (QLD 1516); 1♂, AM P61797 (QLD 1517); 2♀♀, AM P61798 (QLD 1519); 1♂, 1♀, 1 juvenile, AM P61799 (QLD 1520); 1♂, 1♀, AM P61800 (QLD 1522); 1♂, 1 premature female, AM P61801 (QLD 1528); 1♀, AM P61802 (QLD 1529); 1 premature female, AM P61803 (QLD 1531); 1♂, AM P61752 (QLD 1532); 1♀, AM P61805 (QLD 1543); 1♀, AM P61806 (QLD 1549); 1♂, 1♀, AM P61807 (QLD 1553); 1♂, 1♀, AM P61808 (QLD 1554); 1♂, AM P61809 (QLD 1557); >20 specimens, AM P61810 (QLD 1561); 1♂, AM P61811 (QLD 1564); 1♀, AM P61812 (QLD 1568); >20 specimens, AM P61804 (QLD 1570); 1♂, 2♀♀, AM P61813 (QLD 1573); 2♀♀, AM P61814 (QLD 1585); 1♂, 4♀♀, QM W22456, North East Herald Cay, Coringa Herald Nature Reserve, Queensland, Australia, 15°56'S 149°11'E, *Halimeda* sp, 16–20 m, P. Davie & M. Preker, 27 Jun 1997.

Remarks. This species, recently redescribed by Müller (1990), is common in shallow waters of the tropical Indo-Pacific and is clearly the most common species on the Great Barrier Reef. The present specimens are assigned to *Metaprotella sandalensis* on the basis of the arrangement of the dorsal projections and the absence of a marked suture between the head and pereonite 1 (Larsen, 1997). Nevertheless, the great variety of morphological forms and habitats, even in neighbouring populations (as observed at Lizard Island) could reflect polymorphism or indicate the existence of a species complex. Further studies are necessary to investigate if the variation among specimens is intra- or interspecific.

Distribution. Sandal Bay, Lifu, Loyalty Islands (Mayer, 1898); Labuan Badjo, Borneo; Dongala, Celebes; Pulu Tongkil and 6°07.5'N 120°26'E, Sulu Sea; Amboina; between Gisser and Ceram-Laut, Ceram Sea; Singapore, Malaysia; Koh Chang and Koh Kahdal, Thailand; Dutch Bay, Ceylon; Sharks Bay and Cockburn Sound, Australia; Viti Levu, Fiji Islands; Aranuka and Tapeteucea, Gilbert Islands; Ralum, 4°20'S 152°10W; Oahu and Lisiansky Islands, Hawaiian Islands (McCain & Steinberg, 1970); Bora Bora and Moorea, Society Islands (Müller, 1990); Papua New Guinea (Guerra-García, 2003).

Orthoprotella Mayer, 1903

Orthoprotella australis (Haswell, 1880)

Fig. 45

Protella australis Haswell, 1880: 276, pl. 12: fig. 4; Haswell, 1885: 997–998, pl. 49: figs. 2–4; Mayer, 1890: 23.

Orthoprotella australis.—Mayer, 1903: 35–36, pl. 1: figs. 23–24, pl. 6: figs. 45, 47–49, pl. 9: figs. 14, 37, 57.

Material examined. >20 specimens, AM P32321 (GBR 43); 1♂, AM P32324 (GBR 46); 1♂, 1♀, 1 juvenile, AM P61692 (QLD 1559); >20 specimens, AM P61693 (QLD 1560); >20 specimens, AM P61694 (QLD 1562); 2♀♀, 2 juveniles, AM P61691 (QLD 1582).

Remarks. *Orthoprotella australis* is easily distinguished from its congeners by the presence of two acute projections on the head. The species seems to be uncommon on the Great Barrier Reef, but large populations were found on hydroids at Lizard Island.

Distribution. Port Jackson, Australia (Haswell, 1880); off Manning River and Port Stephens, Australia; between Gisser and Ceram Laut, Ceram Sea; Pulu Jedan, Arafura Sea; Banda Sea; Sawu Sea (McCain & Steinberg, 1970); a new record for Queensland, Australia.

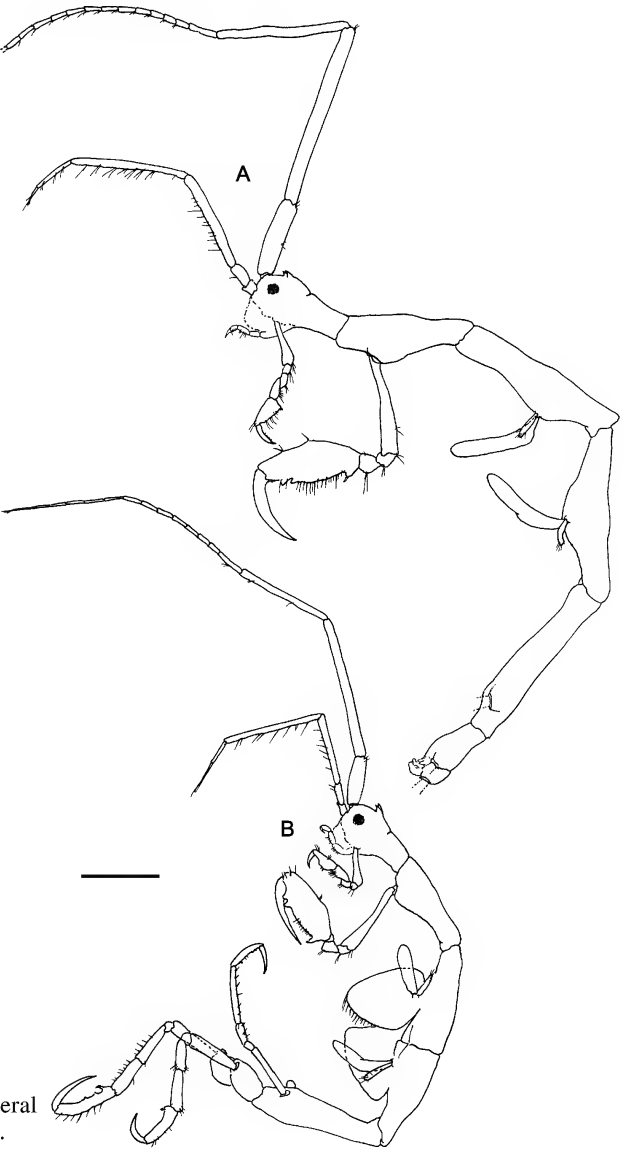


Fig. 45. *Orthoprotella australis* (Haswell, 1880). Lateral view. (*A*) male; (*B*) female. (AM P61693). Scale: 1 mm.

Orthoprotella mayeri Barnard, 1916

Fig. 46

Orthoprotella sp. Mayer, 1903: 36, pl. 1: figs. 25–26, pl.6: figs. 43–44, 46, pl. 9: fig. 15.
Orthoprotella mayeri Barnard, 1916: 284–285; Laubitz, 1991: 118, fig. 14.

Material examined. 2♂♂, AM P61608 (st 20); 1♂, AM P61609 (st 23); 1♂, AM P61607 (st 30); 1♀, (QLD 1570).

Remarks. *Orthoprotella mayeri* was figured recently by Laubitz (1991) based on specimens from New Caledonia.

Distribution. South Africa (Barnard, 1916); Sydney, Australia; Singapore, Malaysia (McCain & Steinberg, 1970); New Caledonia (Laubitz, 1991); a new record for Queensland, Australia.

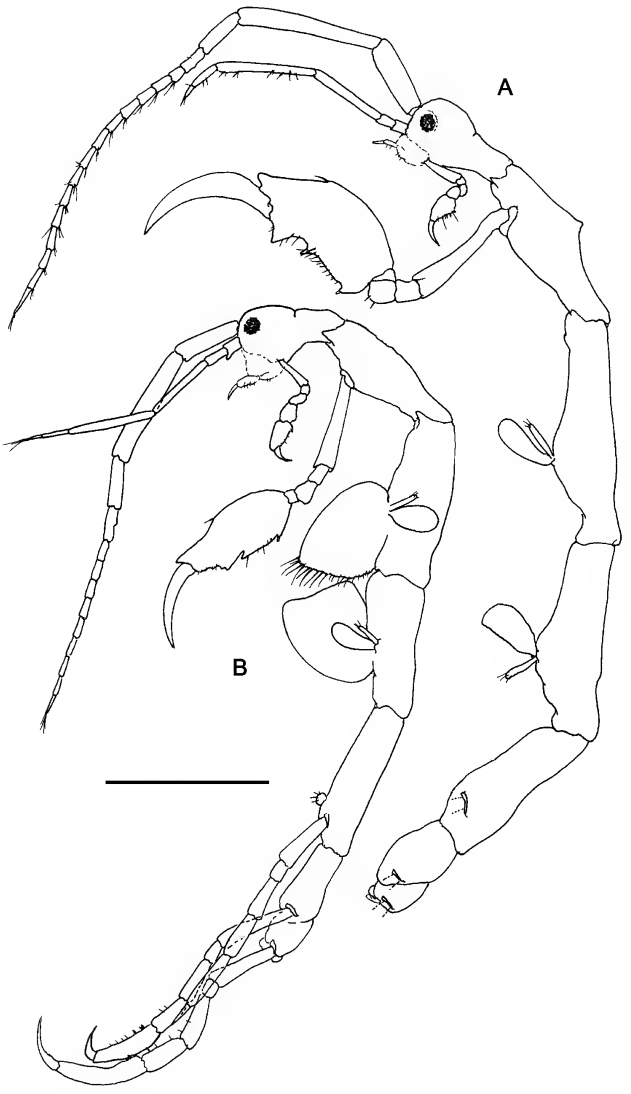


Fig. 46. *Orthoprotella mayeri* Barnard, 1916. Lateral view. (*A*) male (AM P61608); (*B*) female (QLD 1570). Scale: 1 mm.

Orthoprotella pearce n.sp.

Figs 47–51

Type material. HOLOTYPE ♂, AM P61740, Pidgin Point, Lizard Island, Queensland, on hydroid *Halopteris buskii*, 5–10 m, QLD 1580, J.M. Guerra-García & S.J. Keable, 18 Oct 2001. PARATYPES: 1♀, AM P61741, type locality; 5♂♂, 2♀♀, 4 juveniles, AM P61742, type locality; 2♀♀, 1 juvenile, AM P61743, Coconut Beach, Lizard Island, Queensland, on hydroid *Macrorhynchia philippina*, 4 m, QLD 1474, J.M. Guerra-García & S.J. Keable, 8 Oct 2001.

Etymology. This species is dedicated to Marianne and Lance Pearce, the accommodation and maintenance officers of Lizard Island Research Station, for help, encouragement and hospitality during the field study at Lizard Island; used as a noun in apposition.

Diagnosis. A pair of anterolateral projections on pereonites 2–4 in males and 2–3 in females. Distal article of the mandibular palp with a setal formula 1-x-1, being x=7. Distal projection of the third article of maxilliped palp absent. Pereopods 3 and 4 uniarticulate. A pair of 2-articulate abdominal appendages in males.

Description

Holotype male. • *Body length*. 5.6 mm. • *Lateral view* (Figs 47A). Body smooth except for three pairs of lateral acute projections on pereonites 2–4. Pereonites 3 and 4 subequal in length; pereonite 7 the shortest. • *Gills* (Fig. 47A). Present on pereonites 3–4, elongate, length almost 3 times width. • *Mouthparts*. Upper lip (Fig. 48B) symmetrically bilobed, not setose apically. Mandibles (Fig. 49A,B) with 3-articulate palp; distal article of palp with nine setae following the formula 1-x-1, being x=7; second article of the palp with three setae on the right mandible (Fig. 49A) and two setae on the left mandible (Fig. 49B); mandibular molar present, bordered by robust teeth; left mandible with incisor 5-toothed, lacinia mobilis 5-toothed followed by three plumose setae; incisor of right mandible 5-toothed, lacinia mobilis serrate, followed by two plumose setae; molar flake present on right mandible with short setulae distally. Lower lip (Fig. 48C) with inner lobes clearly smaller than outer lobes, well demarcated; inner and outer lobes smooth. Maxilla 1 (Fig. 48D) outer lobe with seven robust setae, serrate laterally; distal article of palp with four apical robust setae and a row of four setae medially. Maxilla 2 (Fig. 48E) inner lobe with six setae distally; outer, about 1.3 times as long as inner lobe, with six apical setae. Maxilliped (Fig. 48A) inner plate rectangular with one nodular robust and short setae and three simple setae; outer plate large, about 3 times as long as inner plate, with one acute seta apically and six setae laterally; margin distally crenulated; palp four-articulate, setose, dactylus with rows of setulae. • *Antennae*. Antenna 1 (Fig. 50A) about ⅔ body length; distal article of the peduncle short, about ⅓ length of preceding article; flagellum 1 3-articulate. Antenna 2 (Fig. 50B) about half width of antenna 1; swimming setae absent; proximal article of the peduncle with a distal projection; flagellum 2-articulate. • *Gnathopods*. Gnathopod 1 (Fig. 50C) basis as long as ischium, merus and carpus combined; merus and carpus setose; propodus setose, length about 1.5 times width, palm with a row of minute setulae proximally, one pair of grasping spines, followed by a row of five smaller grasping

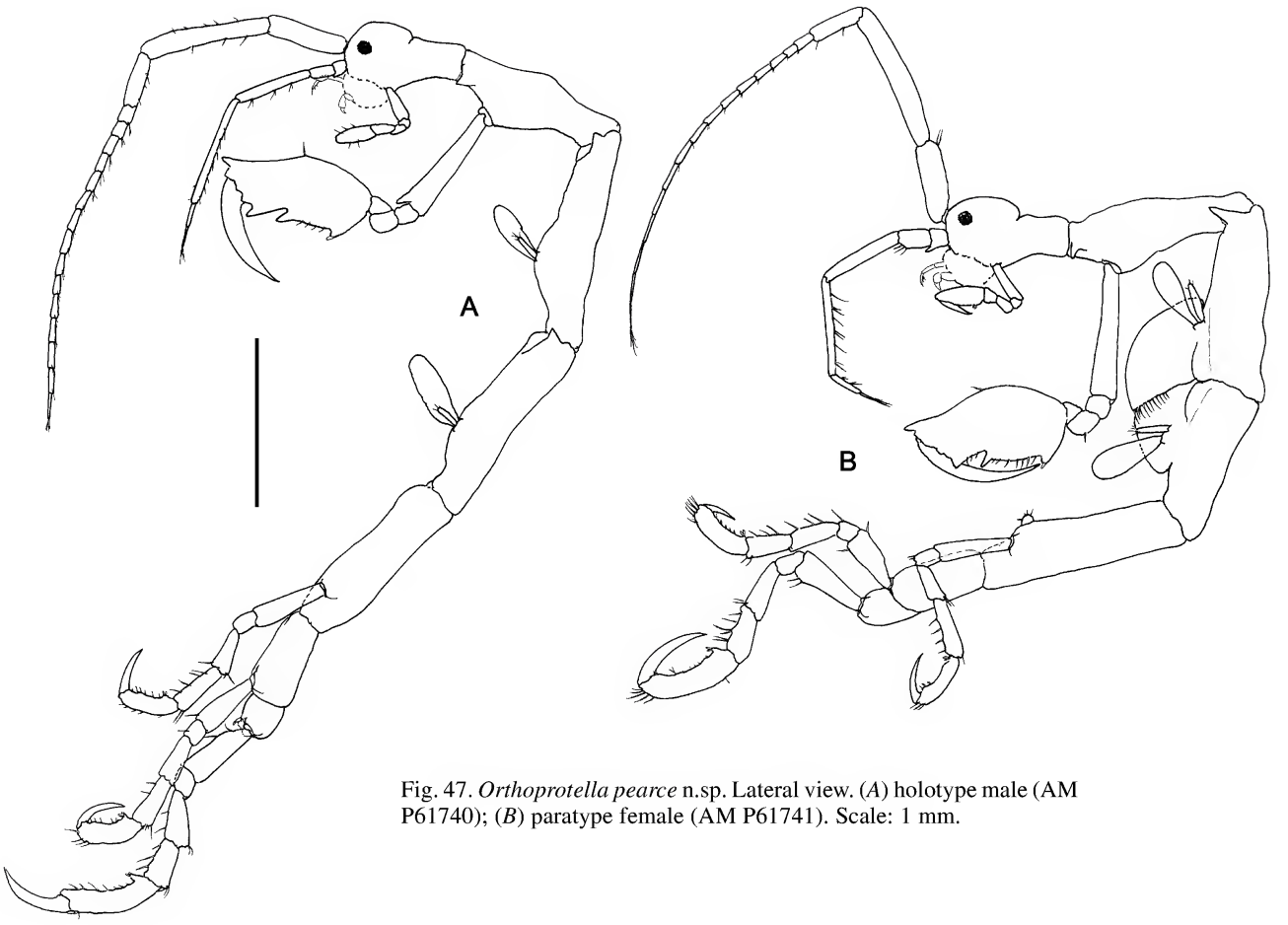


Fig. 47. *Orthoprotella pearce* n.sp. Lateral view. (*A*) holotype male (AM P61740); (*B*) paratype female (AM P61741). Scale: 1 mm.

spines and four setae; dactylus with a dorsal setae proximally and two lateral setae on the distal end, which is divided. Gnathopod 2 (Fig. 50D) inserted on the anterior part of pereonite 2 (Fig. 47A); basis about ¾ as long as pereonite 2, with acute distal projection; ischium rectangular with a small rounded projection; merus rounded; carpus triangular; propodus about 1.2 times as long as basis, with acute distal projection dorsally, palm provided with one grasping spine proximally, followed by several setae and U-notch; dactylus elongate and curved, smooth. • *Pereopods*. Pereopods 3 and 4 reduced (Fig. 51A,B) about ⅓ as long as gills, one-articulate, provided with five setae. Pereopods 5–7 (Fig. 51C–E) six articulate, palm of the propodus with a pair of grasping spines. • *Penes*. (Fig. 51F) Small, rounded, as long as wide. • *Abdomen*. (Fig. 51F) With a pair of appendages and single dorsal lobe; appendages 2-articulate, positioned on setose peduncles (which are projections of the body); proximal article elongate, with small distal setulae; distal article about ⅕ as long as proximal article, with two apical setae; dorsal lobe with two plumose setae.

Paratype female. • *Body length* 5.4 mm. Lateral projections on pereonite 4 lacking (Fig. 47B). Oostegites on pereonite 3 setose, on pereonite 4 not setose (Fig. 47B). Gnathopod 2 similar to male (Fig. 50E). Abdomen (Fig. 51G) without appendages.

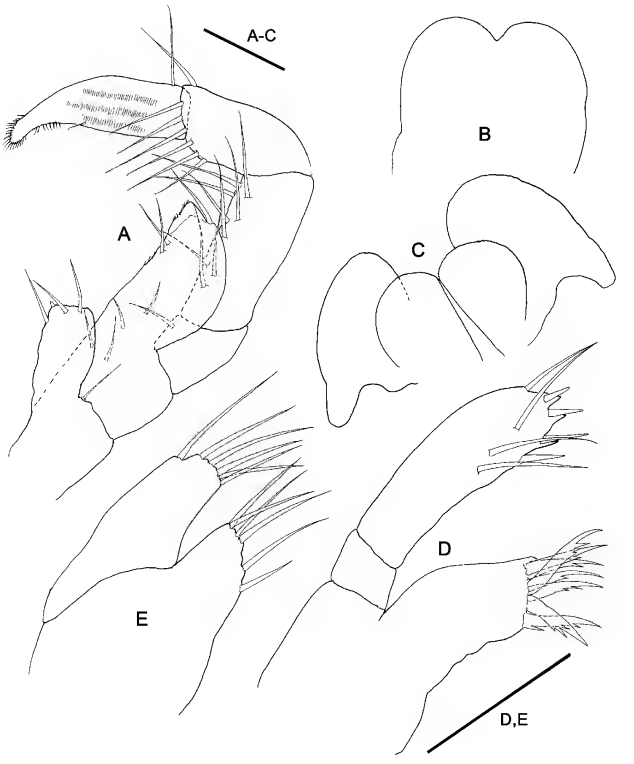


Fig. 48. *Orthoprotella pearce* n.sp. Holotype male (AM P61740). (*A*) maxilliped; (*B*) upper lip; (*C*) lower lip; (*D*) maxilla 1; (*E*) maxilla 2. Scales 0.05 mm.

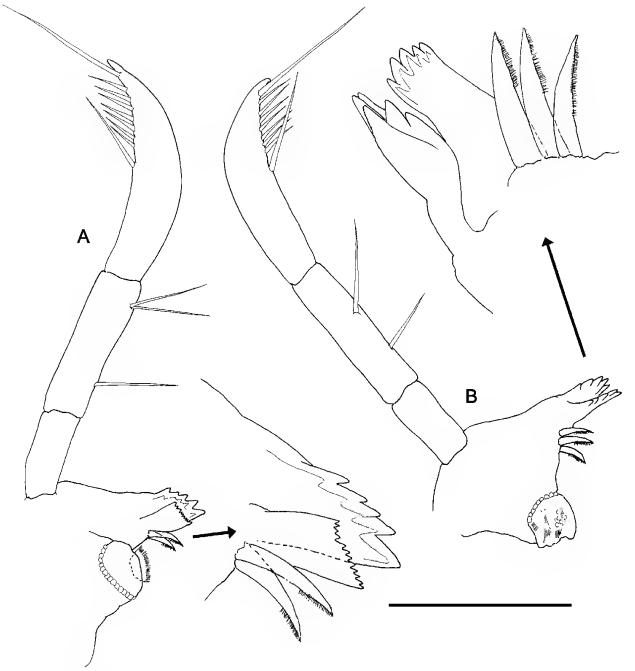


Fig. 49. *Orthoprotella pearce* n.sp. Holotype male (AM P61740). (*A*) right mandible; (*B*) left mandible mandible. Scale: 0.1 mm.

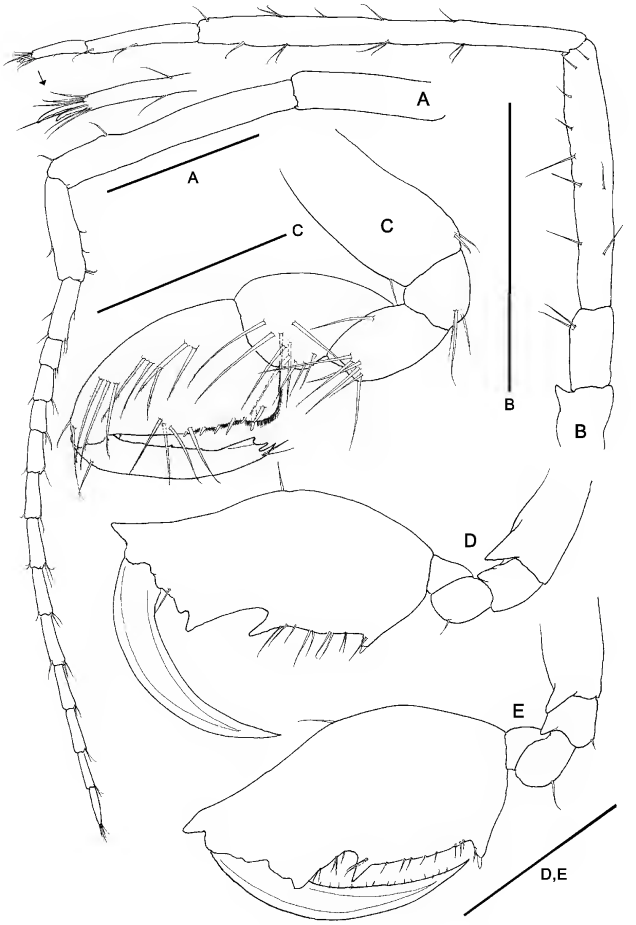


Fig. 50. *Orthoprotella pearce* n.sp. (*A–D*) holotype male (AM P61740). (*A*) antenna 1; (*B*) antenna 2; (*C*) gnathopod 1; (*D*) gnathopod 2; (*E*) paratype female (AM P61741) gnathopod 2. Scales: A,B,D,E: 0.5 mm; C: 0.2 mm.

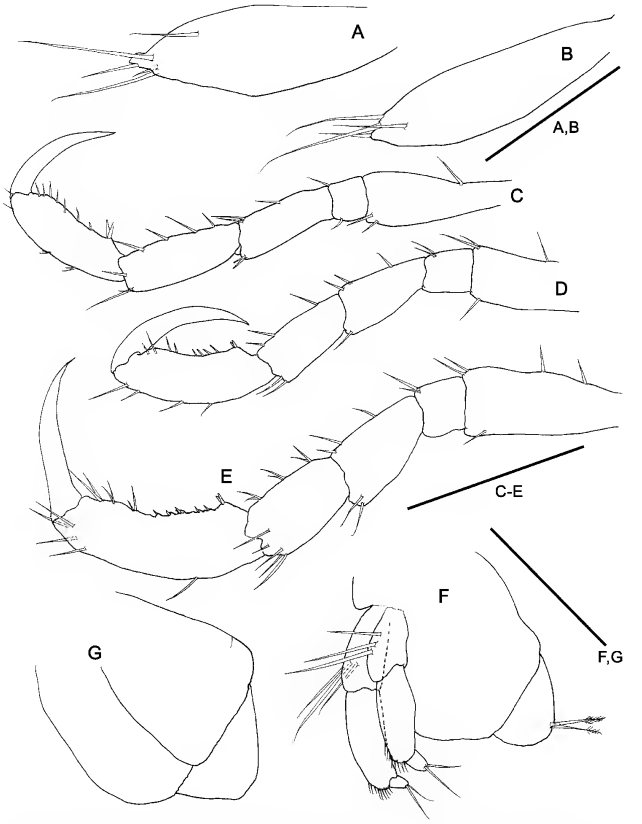


Fig. 51. *Orthoprotella pearce* n.sp. (*A–F*) holotype male (AM P61740). (*A*) pereopod 3; (*B*) pereopod 4; (*C*) pereopod 5; (*D*) pereopod 6; (*E*) pereopod 7; (*F*) abdomen (lateral view); (*G*) paratype female (AM P61741) abdomen (ventral view). Scales: *A,B,F,G*: 0.1 mm; *C,D*: 0.5 mm.

Remarks. The new species of *Orthoprotella* is close to *O. mayeri* and they can be distinguished only with observation of the lateral view and careful examination of the mouthparts. *Orthoprotella mayeri* presents the pereopods 3 and 4 as 2-articulate, although the distal article is tiny and difficult to detect, whilst in *O. pearce* these pereopods are uni-articulate. In connection with the mouthparts, the distal article of the mandibular palp in *O. mayeri* presents a setal formula 1-x-y-1 being x>20 and y=2-4, while the formula in *O. pearce* is 1-x-1 with x=7; furthermore, the distal projection of the third article of the maxilliped palp, present in *O. mayeri*, is absent in *O. pearce*.

Distribution. Presently known only from Lizard Island, Queensland.

Paracaprella Mayer, 1890

Paracaprella sp.

Fig. 52

Material examined. 1 premature female, AM P61633 (QLD 659); 2 premature females, AM P61634 (QLD 658); 1♀, AM P61646 (QLD 921); 2 juveniles, AM P61825, Lucinda, Queensland, 18°31'S 146°19'E, on driftwood on muddy sand flat, P. Colman, 1 Jun 1977.

Remarks. Only females and juveniles have been recorded of this species. The specimens have been assigned to the genus *Paracaprella* on the basis of the combination of the following features: antenna 2 flagellum 2-articulate, mandibular palp reduced, molar present, gills on pereonites 3 and 4, pereopods 3 and 4 2-articulate and pereopods 5–7 six-articulate. Species level identification was not possible owing to the absence of male specimens.

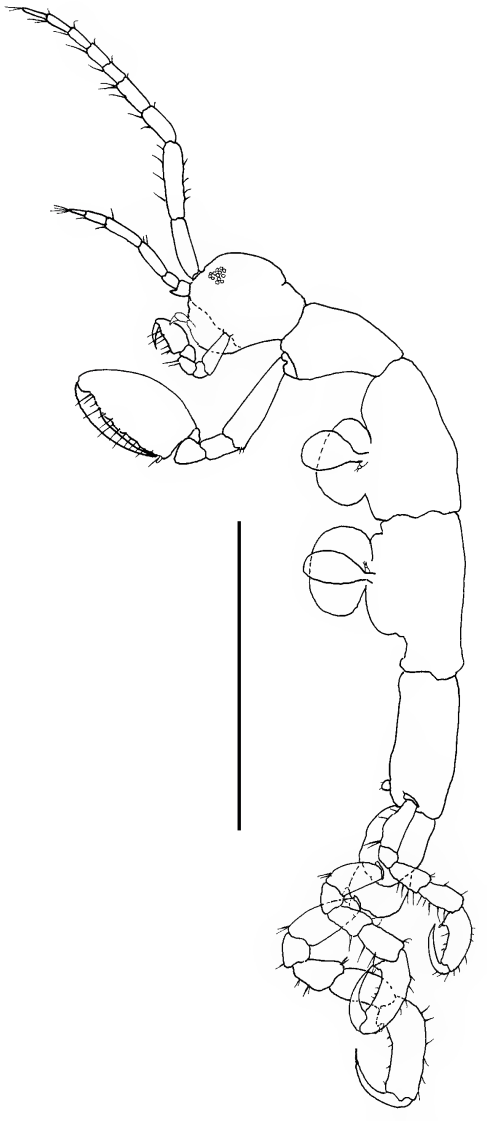


Fig. 52. *Paracaprella* sp. Premature female (AM P61633), lateral view. Scale: 1 mm.

Protella Dana, 1852

Protella similis Mayer, 1903

Fig. 53

Protella similis Mayer, 1903: 34–35, pl. 1: figs. 19–22, pl. 6: figs. 41–42; Laubitz, 1991: 119, fig. 16; Guerra-García, 2002b: 227–229, figs. 13–16.

Material examined. 1♀, AM P32305 (GBR 7); >20 specimens, AM P61704 (QLD 1505); 1♀, 3 juveniles, AM P61705 (QLD 1507); 2♂♂, AM P61706 (QLD 1511); >20 specimens, AM P61707 (QLD 1525); 2♀♀, AM P61708 (QLD 1527); >20 specimens, AM P61709 (QLD 1546); >20 specimens, AM P61710 (QLD 1547); >20 specimens, AM P61711 (QLD 1579).

Remarks. Laubitz (1991) figured the species based on Philippine material, and Guerra-García (2002b) redescribed and figured in detail a female collected from Tanzania. The specimens examined from Lizard Island are in agreement with previous descriptions. As with *Orthoprotella australis*, although the species seems uncommon on the Great Barrier Reef, it can be locally abundant living mainly on hydroids.

Distribution. Indonesia (Mayer, 1903); Philippines (Laubitz, 1991); Tanzania (Guerra-García, 2002b); a new record for Australia.

Pseudaeginella Mayer, 1890

Pseudaeginella biscaynensis (McCain, 1968)

Fig. 54

Fallotritella biscaynensis McCain, 1968: 58–61, figs. 27–28, 53.—McCain & Steinberg, 1970: 51.—Gable & Lazo-Wasem, 1987: 637–638.
Pseudaeginella biscaynensis.—Laubitz, 1995: 88.

Type material. HOLOTYPE ♂, USNM 120179, Bear Cut, Key Biscayne, Florida, 2 m. Allotype female, USNM 120180, type locality. PARATYPES: 6♂♂, USNM 120183–186, 120188, type locality; 3♀♀, USNM 120182, 120187, type locality.

Additional material examined. 1♂, AM P61620 (QLD 680); 1♂, AM P61621 (QLD 734); 1♀, AM P61623 (QLD 759); 2♂♂, AM P61622 (QLD 760); 3♂♂, 1♀, AM P61583 (st 21); 1♂, 1♀, AM P61584 (st 36); 3♂♂, 6♀♀, 4 juveniles, AM P61585 (st 14); 1♂, AM P61586 (st 8); 1♂, AM P61689 (BK-114); 1 premature female, AM P61688 (BK-126); 1 premature female, AM P61690 (QLD 1476).

Remarks. Recently, Laubitz (1995) considered *Fallotritella* to be synonymous with *Pseudaeginella*, based mainly on the presence of minute pereopods 3 and 4 also in *Pseudaeginella*. Consequently, *P. biscaynensis, P. montouchetti* and *P. polynesica*, previously placed in *Fallotritella*, were transferred to *Pseudaeginella*. The Queensland specimens agree with the type material from Florida, apart from differences in body projections and pereopod 5. The specimens from Queensland have a more robust pereopod 5 and are considerably less spinose than the type specimens. Nevertheless, the type material shows a considerable degree of morphological variability and consequently the present specimens of *Pseudaeginella* are assigned to *P. biscaynensis*. *Pseudaeginella biscaynensis*, known from the Florida coast and vicinity, has also been recently recorded in the Indian Ocean (Guerra-García, 2002b). Hence, the species is probably cosmopolitan but

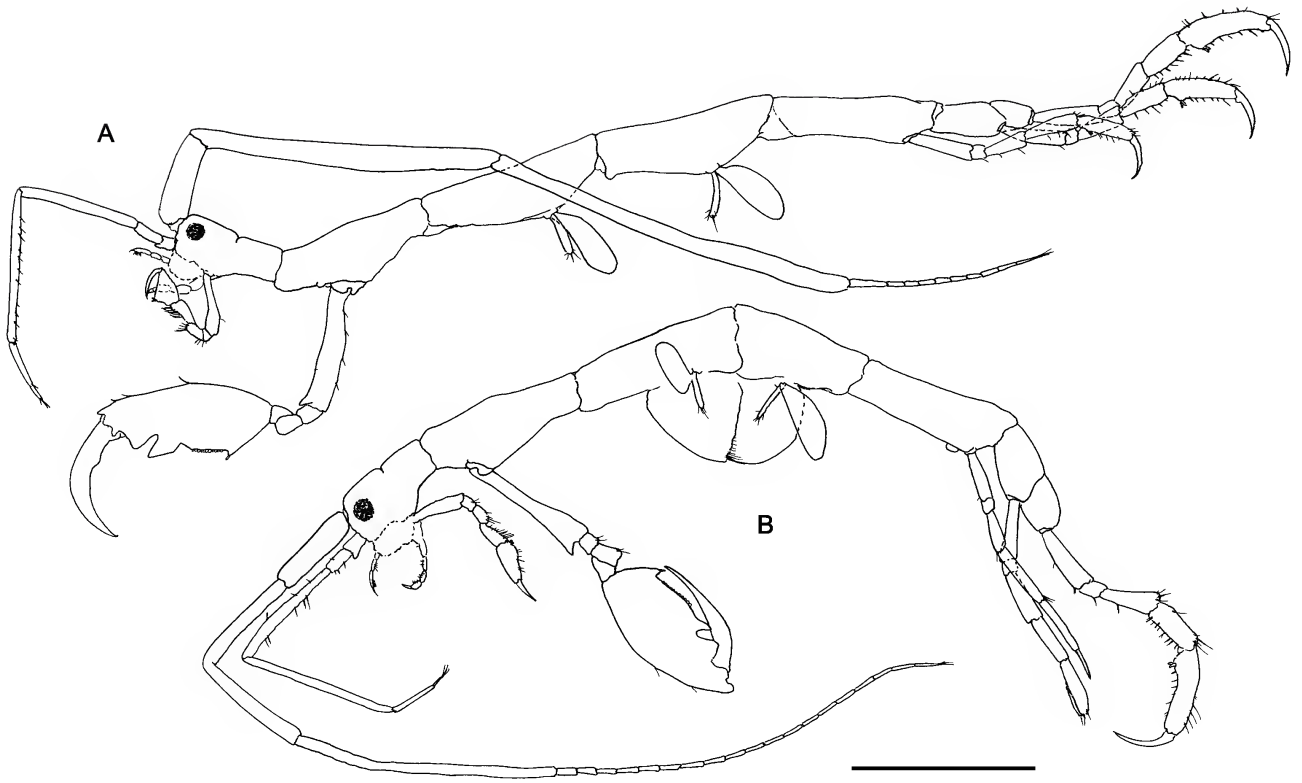


Fig. 53. *Protella similis* Mayer, 1903. Lateral view. (*A*) male; (*B*) female. (AM P61707). Scale: 1 mm.

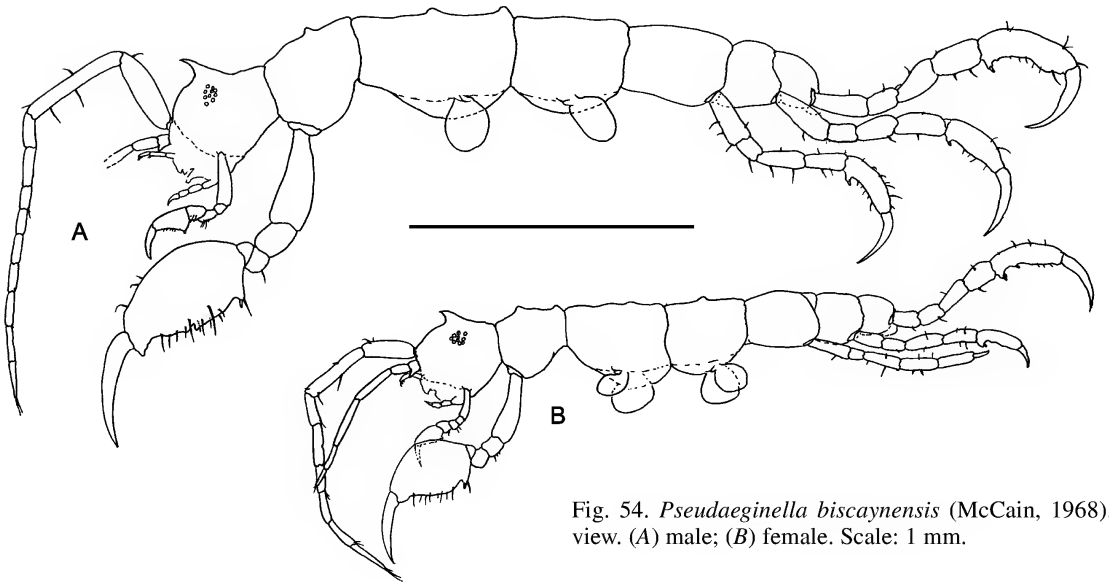


Fig. 54. *Pseudaeginella biscaynensis* (McCain, 1968). Lateral view. (*A*) male; (*B*) female. Scale: 1 mm.

the general paucity of worldwide records probably owes to its small body size and usual detritus covering. Nevertheless, it remains that *P. biscaynensis* may prove to be a species complex. This problem is rather common in the Caprellidae (e.g., *Caprella penantis, Caprella scaura, Metaprotella sandalensis*). Further study of these species is required.

Distribution. Bear Cut, Key Biscayne, Florida; Bermuda; Soldier Key, Key Largo and Long Key, Florida; Tortugas; Barbuda; Pigem Island, Santa Lucia (McCain, 1968; Gable & Lazo-Wasem, 1987); Tanzania (Guerra-García, 2002b); and Papua New Guinea (Guerra-García, 2003); a new record for Australia.

Field study at Lizard Island

Habitat use. The semi-qualitative abundance of caprellids found at Lizard Island in each habitat is summarized in Table 1. The caprellids, although present in the majority of the samples collected, were not abundant in coral habitats of Lizard Island. Only the hydroids and the sediments presented high values of richness and abundances of the Caprellidae.

Metaprotella sandalensis and *Quadrisegmentum triangulum* were the most common species around the Island, being present in the majority of substrates on both hard and soft bottoms. Conversely, the majority of the species were found only in specific habitats. *Pseudaeginella biscaynensis, Hemiaegina minuta, Orthoprotella mayeri*, and *Orthoprotella pearce* n.sp. were found only on hydroids. *Metaproto novaehollandiae, Perotripus keablei* n.sp., *Protogeton inflatus* and *Pseudoprellicana johnsoni* were restricted to sediments and/or coral rubble. *Aciconula australiensis, Pseudoproto fallax* and *Jigurru vailhoggett* were found clinging to the algal turf growing on dead hard corals. The cluster analysis based on the habitat use showed different groups of species (Fig. 55).

Recently Guerra-García (2001) conducted a similar ecological study in Ceuta, North Africa, a temperate enclave in the Strait of Gibraltar. With a coastline of about 20 km, Ceuta is approximately the same size as Lizard Island. The benthic communities around Ceuta, as of a typical temperate region, are dominated by algae beds in the shallow waters (instead of corals, which are dominant in the tropics) and hydroids, gorgonians, sponges and ascidians in the deeper areas (see Guerra-García, 2001). Guerra-García (2001) collected samples of different substrates along the coast of Ceuta (algae, hydroids, sponges, gorgonians, bryozoans, ascidians and sediments). A summary of the data is given in Table 2. Comparison of data from Ceuta with that of Lizard Island indicates that the number of species is similar in both regions (22 species in Ceuta, 16 species in Lizard Island). Nevertheless, in spite of similar species richness, there are important differences in the caprellid community between the two localities: (*a*) at Ceuta the species are distributed in only 5 genera with most in *Caprella*, whereas at Lizard Island 13 genera are represented, none of which belong to *Caprella*; (*b*) although caprellids are frequent in both areas, the abundance values are clearly higher at Ceuta than at Lizard Island; (*c*) the highest species richness and abundance of caprellids was found on algae and hydroids at Ceuta whereas caprellids are practically absent on the algae from Lizard Island. Although the algae species differ between temperate and tropical regions, species with similar morphology are found in both places. In spite of collecting 45 algal samples comprising 20 species around Lizard Island, only two caprellid species were found: *Mayeri-caprella sandalensis* and *Q. triangulum*, being the most common species found on all substrates along the coral reef system. The reason for this distribution is not clear. The different degree of algae cover in both systems might be involved: the algae cover is much higher in temperate than tropical regions, which are instead dominated by corals. Nevertheless, the hydroid cover is not so high on coral reefs, although the hydroids registered the highest species richness and abundance of the Caprellidae. Perhaps the activity of predators could be significantly different. Caprellids are considered important prey for many fish species (Caine, 1987, 1989, 1991) and the abundance of fishes in tropical areas is high. Taking into account that many of the coral reef hydroids are stinging species, it would be possible that the caprellids use hydroid habitats as a protection instead of using algae where they are potentially less protected from fish predators. This could explain the general low abundance of caprellids on coral reefs but the specific higher abundances registered on the stinging hydroids. Future studies are necessary to elucidate ecological patterns and habitat preferences of the Caprellidae along the coral reef systems of tropical areas.

Distribution of the Caprellidae around Lizard Island. Guerra-García & García-Gómez (2001) showed that the caprellid community at Ceuta could be used as a bioindicator of environmental conditions because the distribution of caprellids is highly influenced by physico-chemical factors such as hydrodynamics. In the present study, using multivariate analysis, when comparing the caprellid fauna in the different sites around the island (Table 3), found no clear differences between the west and the east coast (Fig. 56). Although MDS seems to separate the two groups of

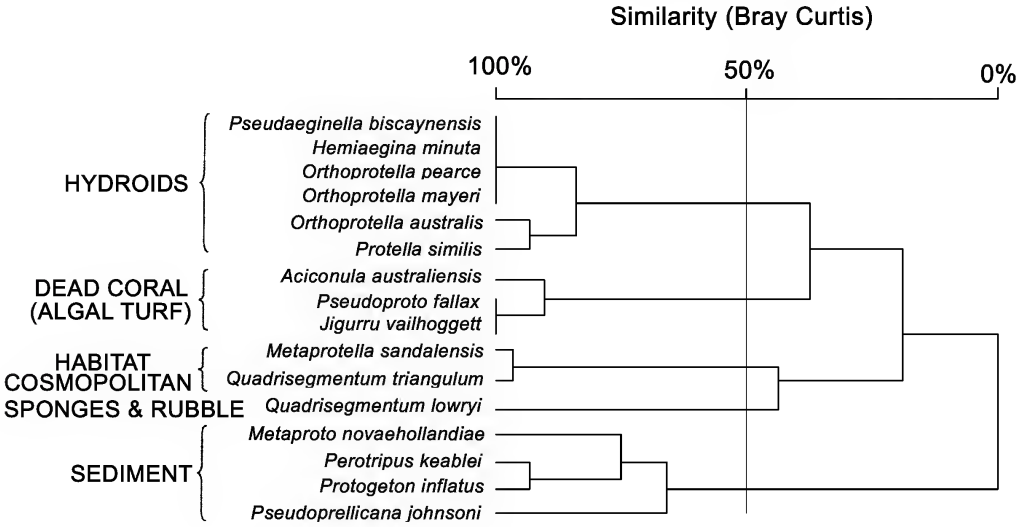


Fig. 55. Dendrogram of similarity between the different caprellid species in base of the habitat preferences (see Table 1).

Table 2. Species composition of the Caprellidae from Ceuta, northern Africa (temperate region). The qualitative values of abundance of caprellids in the different habitats are included. Qualitative scale: white, absent; • rare (1–10 individuals/sample); •• common (10–100 ind/sample); ••• very common (>100 ind/sample). Information taken from Guerra-García (2001).

	algae	sponges	hydroids	gorgonians	bryozoans	ascidians	biodetritic	coarse shelly sediment	fine sediment
Caprella acanthifera Leach, 1814	••	•	•	•	•	•	○	•	○
C. acanthifera discrepans (see Krapp-Schickel & Vader, 1998)	••	○	•	○	○	•	○	○	○
C. cavediniae Krapp-Schickel & Vader, 1998	○	○	•	○	○	○	○	○	○
C. ceutae Guerra-García & Takeuchi, 2002	○	○	•	○	○	○	○	○	○
C. danilevskii Czerniavskii, 1868	•••	○	○	○	○	○	○	○	○
C. dilatata Kröyer, 1843	•	○	○	○	○	○	○	○	○
C. erethizon Mayer, 1901	○	○	••	○	○	•	○	○	○
C. fretensis Stebbing, 1878	•	○	○	○	○	○	○	○	○
C. grandimana Mayer, 1882	•	○	○	○	○	○	○	○	○
C. hirsuta Mayer, 1890	•	○	○	○	○	○	○	○	○
C. liparotensis Haller, 1879	••	○	•	○	○	○	○	○	○
C. monai Guerra-García, Sánchez-Moyano & García-Gómez, 2001	○	○	•	○	○	○	○	○	○
C. penantis Leach, 1814	•••	○	•	○	○	○	○	•	○
C. sabulensis Guerra-García, Sánchez-Moyano & García-Gómez, 2001	○	○	○	○	○	○	•	○	○
C. santosrosai Sánchez-Moyano, Jiménez-Martín & García-Gómez, 1995	○	•	•••	•	○	○	○	○	○
C. takeuchii Guerra-García, Sánchez-Moyano & García-Gómez, 2001	•	○	○	○	○	○	○	○	○
C. tuberculata Bate & Westwood, 1868	○	○	•	○	○	○	○	○	○
Pariambus typicus Kröyer, 1844	○	○	○	○	○	○	••	••	•••
Pedoculina garciagomezi Sánchez-Moyano, Carballo & Estacio, 1995	•	○	○	○	○	○	○	○	○
Phtisica marina Slabber, 1769	•••	•	••	••	••	••	••	••	•••
Pseudoprotella inermis Chevreux, 1927	○	○	•	○	○	○	○	○	○
P. phasma (Montagu, 1804)	•••	○	•••	••	○	○	○	•	•

stations according to the caprellid composition, this ordination is not clear in the dendrogram of the Cluster analysis (Fig. 56).

These results could indicate that environmental conditions such as hydrodynamics, silting, and suspended organic matter in the water column are not radically different on both sides of the Island as one might expect from the exposure to the strong winds from the southeast from mid-March to September each year. Although some current speed measurements are given by Leis (1986), a complete study of the environmental conditions of the shallow waters around the Island would be necessary to test whether or not the physico-chemical differences between the west and east coasts are significant.

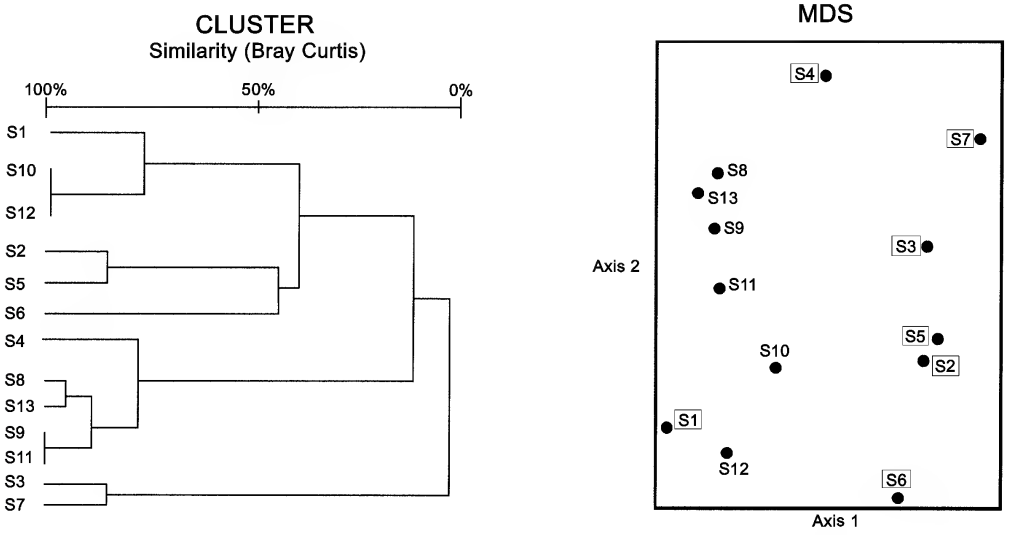


Fig. 56. MDS analysis and dendrogram of similarity between the stations sampled on SCUBA (see Fig. 2) in base of the caprellid composition.

Table 3. Species compositions of the Caprellidae in the 13 stations sampled on SCUBA at Lizard Island and used for the multivariate analysis of ordenation and classification (Fig. 55). (•, presence; ○, absence).

	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13
Aciconula australiensis	○	•	•	○	•	○	○	○	○	○	○	○	○
Hemiaegina minuta	○	•	○	○	○	○	○	○	○	○	○	○	○
Jigurru vailhoggett	○	○	○	○	•	○	○	○	○	○	○	○	○
Metaprotella sandalensis	•	•	•	○	•	•	○	•	•	•	•	•	•
Metaproto novaehollandiae	○	•	•	○	○	•	•	○	○	○	○	○	•
Orthoprotella australis	○	○	○	•	○	•	○	○	○	○	○	○	○
Orthoprotella mayeri	○	•	○	○	○	○	○	○	○	○	○	○	○
Orthoprotella pearce	○	○	○	•	•	○	○	○	○	○	○	○	○
Perotripus keablei	○	○	○	○	○	○	•	○	○	○	○	○	○
Protella similis	○	○	○	•	○	○	○	•	•	○	•	○	•
Protogeton inflatus	○	○	○	•	○	○	○	○	○	○	○	○	○
Pseudaeginella biscaynensis	○	•	○	○	•	○	○	○	○	○	○	○	○
Pseudoprellicana johnsoni	○	○	○	○	○	•	○	○	○	○	○	○	○
Pseudoproto fallax	○	○	•	○	•	○	○	○	○	○	○	○	○
Quadrisegmentum lowryi	○	○	○	○	○	○	○	•	○	○	○	○	○
Quadrisegmentum triangulum	○	•	•	•	•	○	•	•	•	•	•	○	○

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Appendix. List of stations.

BK-113 Patch Reefs off Palfrey Island, Lizard Island, Queensland, rubble in depressions between coral heads, collected by hand on SCUBA, 8 m, B. Kensley, 10 Jan 1982.

BK-114 North Point, Lizard Island, Queensland, fine filamentous algae, collected by hand on SCUBA, 2 m, B. Kensley, 11 Jan 1982.

BK-126 Reef flat between Bird and South Island, Lizard Island, Queensland, fuzzy red algae, collected by hand on SCUBA, 3 m, B. Kensley, 16 Jan 1982.

BK-127 Crest of Patch Reef in Lizard Island Lagoon, Lizard Island, Queensland, rubble with algal turf taken from the depressions on crest, collected by hand on SCUBA, 8 m, B. Kensley, 16 Jan 1982.

GBR 1 off Mangrove Beach, Lizard Island, Queensland, 14°40'S 145°28'E, mixed algae from bommie, 2 m, J.K. Lowry, 28 Sep 1978.

GBR 5 Lagoon, Lizard Island, Queensland, 14°41'S 145°28'E, 1.5 m, C. Short & P.C. Terrill, 30 Sep 1978.

GBR 6 off Mangrove Beach, Lizard Island, Queensland, 14°40'S 145°28'E, sand, 1.5 m, C. Short & A.R. Jones, 30 Sep 1978.

GBR 7 Between Mangrove Beach & South Island, Lizard Island, Queensland, 14°40'S 145°28'E, sand, 9 m, J.K. Lowry & P.C. Terrill, 30 Sep 1978.

GBR 10 off south end Casuarina Beach, Lizard Island, Queensland, 14°40'S 145°28'E, beach sand, low water mark, J.K. Lowry, 4 Oct 1978.

GBR 11 west end lagoon, Lizard Island, Queensland, 14°40'S 145°28'E, algae *Halimeda micronesica, Caulerpa racemosa*, 3 m, J.K. Lowry, C. Short & P.C. Terrill, 5 Oct 1978.

GBR 12 Lagoon, Lizard Island, Queensland, 14°40'S 145°28'E, mixed algae from artificial reef cages, *Lynbya* sp., 4.5 m, P.C. Terrill, 5 Oct 1978.

GBR 14 Between Bird Islet & Trawler Beach, Lizard Island, Queensland, 14°40'S 145°28'E, sand, 15 m, J.K. Lowry & P.C. Terrill, 5 Oct 1978.

GBR 15 Between Bird Islet & South Island, Lizard Island, Queensland, 14°40'S 145°28'E, coral rubble, 21 m, A.R. Jones, 7 Oct 1978.

GBR 19 Between Bird Islet & South Island, Lizard Island, Queensland, 14°40'S 145°28'E, coral rubble, 6 m, P.C. Terrill, 7 Oct 1978.

GBR 20 Between Bird Islet & South Island, Lizard Island, Queensland, 14°40'S 145°28'E, coral rubble, 6 m, J.K. Lowry, 7 Oct 1978.

GBR 21 Between Bird Islet & South Island, Lizard Island, Queensland, 14°40'S 145°28'E, *Halophila, Caulerpa, Halimeda*, 25.5 m, J.K.Lowry, 7 Oct 1978.

GBR 25 off southern point Mermaid Cove, Lizard Island, Queensland, 14°40'S 145°28'E, filamentous algae, sediment, 5 m, C. Short & P.C Terrill, 8 Oct 1978.

GBR 26 Mermaid Cove, Lizard Island, Queensland, 14°41'S 145°28'E, sand between corals, 6 m, C. Short & P.C. Terrill, 8 Oct 1978.

GBR 27 Between Bird Islet & South Island, Lizard Island, Queensland, 14°40'S 145°E, sediment at reef base with mixed algae, 25 m, J.K. Lowry, 9 Oct 1978

GBR 28 Between Bird Islet & South Island, Lizard Island, Queensland, 14°40'S 145°28'E, sediment at reef base with mixed algae 25 m, P.C. Terrill, 9 Oct 1978

GBR 29 Between Bird Islet & South Island, Lizard Island, Queensland, 14°41'S 145°28'E, sediment at reef base with mixed algae, 25 m, J.K. Lowry, 9 Oct 1978.

GBR 30 Between Bird Islet & South Island, Lizard Island, Queensland, 14°40'S 145°28'E, mixed algae, sediment from grassbeds, 25 m, P.C. Terrill, 9 Oct 1978.

GBR 33 western end Lagoon, Lizard Island, Queensland, 14°40'S 145°28'E, sand, 3 m, P.C. Terrill, 15 Oct 1978.

GBR 43 Between Bird Islet & Trawler Beach, Lizard Island, Queensland, 14°40'S 145°28'E, sand, algae, 10 m, P.C. Terrill, 15 Oct 1978.

GBR 44 Off Chinamans Ridge, Lizard Island, Queensland, 14°40'S 145°28'E, sand, mixed algae, 21 m, J.K. Lowry, 13 Oct 1978.
GBR 45 Off Chinamans Ridge, Lizard Island, Queensland, 14°40'S 145°28'E, sand, mixed algae, 21 m, P.C. Terrill, 13 Oct 1978.
GBR 46 Off Chinamans Ridge, Lizard Island, Queensland, 14°40'S 145°28'E, fine sand, 12 m, J.K. Lowry, 13 Oct 1978.
GBR 48 Mermaid Cove, Lizard Island, Queensland, 14°40'S 145°28'E, mixed algae, coral rubble, silt, 2 m, J.K.Lowry, 14 Oct 1978.
GBR 49 Off North Point, Lizard Island, Queensland, 14°40'S 145°28'E, algae, coral rubble, 5 m, J.K.Lowry, 14 Oct 1978.
GBR 50 Off North Point, Lizard Island, Queensland, 14°40'S 145°28'E, mixed algae, 5 m, J.K.Lowry, 14 Oct 1978.
GBR 52 Off North Point, Lizard Island, Queensland, 14°40'S 145°28'E, algae, *Halimeda* sp, 6 m, J.K.Lowry, 14 Oct 1978.
GBR 55 200 m NW of Palfrey Island, Lizard Island, Queensland, 14°40'S 145°28'E, sand beneath coral boulders, 3 m, P.C. Terrill, 16 Oct 1978.
GBR 56 200 m NW of Palfrey Island, Lizard Island, Queensland, 14°40'S 145°28'E, sand 12 m, J.K. Lowry, 16 Oct 1978.
GBR 59 1.6 km SW of Eagle Island, Lizard Island, Queensland, 14°40'S 145°28'E, sediment from coral fans, coral ruble, 6 m, J.K. Lowry, 17 Oct 1978.
GBR 63 1.6 km SW of Eagle Island, Lizard Island, Queensland, 14°40'S 145°28'E, sand, 12 m, A.R. Jones, 17 Oct 1978.
GBR 68 Bommie W of harbour entrance, Heron Island, Queensland, 23°26'S 151°55'E, coarse sand, 21.3 m, J.K. Lowry, 7 Dec 1978.
LHA 11 Between Comet Hole and Reef, Lord Howe Island, assorted red and brown algae with some coral, 2–3 m, J.K. Lowry, 10 May 1977.
LHA 17 Reef front S of North Passage, straight out from Signal Point, between rubble spurs, Lord Howe Island, coralline, 3 m, J.K. Lowry, 11 May 1977.
LHA 48 Old Gulch, Lord Howe Island, lower sides of lower littoral boulders, among algae, G.D. Fenwick, 17 May 1977.
LHA 49 Old Gulch, Lord Howe Island, among algae on mid littoral boulders, J.K. Lowry, 17 May 1977.
LHA 51 Old Gulch, Lord Howe Island, among red algae (*Galaxaria* sp.) on rock, 7 m, J.K.Lowry, 17 May 1977.
St 1 Shallow reef front, Middleton Reef, 29°27.2'S 159°06.8'E, sand and rubble, 10 m, 4 Dec 1987.
St 7 Large alcove near lagoon entrance, Sound dive site, Middleton Reef, 29°27.7'S 159°05.4'E, 6 m, P. Hutchings & I.Loch, 5 Dec 1987.
St 8.1 Shelf Runil Reef, Middleton Reef, 29°27.4'S 159°03.7'E, dead corals, 9–12 m, 5 Dec 1987.
St 10 NE to E outer slope, Middleton Reef, 29°26.1'S 159°08.2'E, 10 m, 6 Dec 1987.
St 12 Patch Reef, Middleton Reef, 29°27.6'S 159°06.7'E, 6 Dec 1987.
St 14 reef near "Fuku Maru" wreck, Middleton Reef, 29°28.8'S 159°07.5'E, 7 Dec 1987.
St 20 Slope off Fuku Maru, Middleton Reef, 29°29.1'S 159°08.1'E, rubble, 15–20 m, 7 Dec 1987.
St 21 Southern slope, between "Runic" and "Fuku Maru", Middleton Reef, 29°29.5'S 159°06.2'E, 15–17 m, 8 Dec 1987.
St 23 Outer slope, W of Runil, Middleton Reef, 29°28'S 159°03.3'E, 9 Dec 1987.
St 30 Outer slope, W of "Yoshin Maru Iwaki", Elizabeth Reef, 29°57.2'S 159°01.2'E, coral rubble, 8–24 m, J.K. Lowry & R.T. Springthorpe, 12 Dec 1987.
St 32 Reef front, Elizabeth Reef, 29°54.8'S 159°02.8'E, algae, 10 Dec 1987.
St 34 SW Outer slope, Elizabeth Reef, 29°57.7'S 159°02.8'E, algae, 11 Dec 1987.
St 36 Off Flamingo Bay, outer slope, southern face, Elizabeth Reef, 29°57.8'S 159°04.7'E, 5 m, P. Hutchings, 11 Dec 1987.
St 37 Outer slope SE face, Elizabeth Reef, 29°58'S 159°05.1'E, 11 Dec 1987.
St 38 Deep lagoon bommie, Elizabeth Reef, 29°56.2'S 159°02.4'E, 10 m, ?fine sediment, 12 Dec 1987.
St 43 Reef flat near Yoshiu Maru Iwaki, Elizabeth Reef, 29°57.2'S 159°01.2'E, J.K Lowry & R.T. Springthorpe, 14 Dec 1987.
St 45 Outer slope near Famingo Bay, on wreck, Elizabeth Reef, 29°56.5'S 159°01.8'E, 7–15 m, 14 Dec 1987
QLD 639 Reef front crest, Great Detached Reef, Queensland, 11°42.17'S 144°1.61'E, *Halimeda*, SCUBA, 9 m, S. Keable, 12 Jan 1993.
QLD 646 Shadwell Reef, Queensland, 11°27.66'S 143°46.63'E, water column, 0 m, H. Larson, J. Leis, McGrouther, 12 Jan 1993.
QLD 650 GBRMPA Reef 11-102, Queensland, 11°27.56'S 143°58. 12'E, living short low clumps of multibranched hard coral, 9 m, S. Keable, 13 Jan 1993.
QLD 651 GBRMPA Reef 11-102, Queensland, 11°27.56'S 143°58. 12'E, coral rubble, 9 m, S. Keable, 13 Jan 1993.
QLD 658 Back reef slope,GBRMPA Reef 11-131, Queensland, 11°26.96'S 144°4.06"E, *Halimeda*, SCUBA, 9 m, S. Keable, 14 Jan 1993.
QLD 659 Back reef flat, GBRMPA Reef 11-131, Queensland, 11°26.96'S 144°4.06E, *Halimeda*, SCUBA, 3 m, S. Keable, 14 Jan 1993.
QLD 660 Back reef flat, GBRMPA Reef 11-131, Queensland, 11°26.96'S 144°4.06E, rubble, SCUBA, 3 m, S. Keable, 14 Jan 1993.
QLD 664 SW end of reef in gully of back reef slope, GBRMPA Reef 11-418, Queensland, 10°59.98'S 144°1.22'E, mixed sponges, SCUBA, 3 m, S. Keable, 15 Jan 1993.
QLD 667 SW end of reef in gully of back reef slope, GBRMPA Reef 11-418, Queensland, 10°59.98'S 144°1.22'E, *Halimeda* and *Caulerpa*, SCUBA, 6 m, S. Keable, 15 Jan 1993.
QLD 668 SW end of reef in gully of back reef slope, GBRMPA Reef 11-418, Queensland, 10°59.98'S 144°1.22'E, coral rubble, SCUBA, 6 m, S. Keable, 15 Jan 1993.
QLD 674 Inside Outer Barrier, Queensland, 10°56.90'S 144°0.51'E, coral rubble, SCUBA, 20 m, S. Keable, 16 Jan 1993.
QLD 675 Small bommie NW of GBRMPA Reef 10-403, Queensland, 10°48.61'S 143°59.36'E, rubble, SCUBA, 16 m, C. Kirby, 16 Jan 1993.
QLD 680 Inside Outer Barrier, Queensland, 10°34.48'S 143°55.28'E, purple sponge, SCUBA, 15 m, S. Keable, 16 Jan 1993.
QLD 683 Inside Outer Barrier, Queensland, 10°34.48'S 143°55.28'E, sediment and loose rubble, SCUBA, 15 m, S. Keable, 16 Jan 1993.
QLD 686 Ashmore Reef, Queensland, 10°26.66'S 144°26.82'E, fine sediment, SCUBA, 15 m, S. Keable, 17 Jan 1993.
QLD 696 Outer reef slope, sheer drop off, Ashmore Reef, Queensland, 10°26.27'S 144°25.78'E, *Halimeda*, SCUBA, 10 m, S. Keable, 18 Jan 1993.
QLD 697 Outer reef face, sheer drop off, Ashmore Reef, Queensland, 10°26.27'S 144°25.78'E, invertebrates, SCUBA, 30 m, S. Keable, 18 Jan 1993.
QLD 703 Outer reef slope, sheer drop off, Ashmore Reef, Queensland, 10°26.27'S 144°25.78'E, rubble, SCUBA, 30 m, S. Keable, 19 Jan 1993.
QLD 704 Outer reef slope, sheer drop off, Ashmore Reef, Queensland, 10°26.27'S 144°25.78'E, red calcareous cylindrical algae, SCUBA, 25 m, S. Keable, 19 Jan 1993.
QLD 705 Outer reef slope, sheer drop off, Ashmore Reef, Queensland, 10°26.27'S 144°25.78'E, sediment, algae and rubble, SCUBA, 12 m, S. Keable, 19 Jan, 1993.
QLD 721 Outer reef slope, sheer walls and caves, Ashmore Reef, Queensland, 10°13.16'S 144°24.89'E, tunicates, SCUBA, 31 m, S. Keable, 22 Jan 1993.
QLD 722 Outer reef slope, Ashmore Reef, Queensland, 10°13.16'S 144°24.89'E, sponges, SCUBA, 25 m, S. Keable, 22 Jan 1993.
QLD 723 Outer reef slope, sheer walls and caves, Ashmore Reef, Queensland, 10°13.16'S 144°24.89'E, rubble, SCUBA, 12 m, S. Keable, 22 Jan, 1993.
QLD 724 Outer reef slope, Ashmore Reef, Queensland, 10°13.16'S 144°24.89'E, consolidated reef with algal turf, SCUBA, 3 m, S. Keable, 22 Jan 1993.
QLD 733 Outer slope, E edge Ashmore Reef, 10°9.16'S 144°34.72'E, rubble, SCUBA, 30 m, S. Keable, 24 Jan 1993.
QLD 734 Outer slope of eastern edge, Ashmore Reef, 10°9.16'S 144°34.72'E, calcareous red tubular algae, SCUBA, 30 m, S. Keable, 24 Jan 1993.
QLD 735 Outer reef slope, E edge Ashmore Reef, 10°9.16'S 144°34.72'E, living coral, SCUBA, 20 m, S. Keable, 24 Jan 1993.
QLD 739 Outer reef slope, E edge Ashmore Reef, 10°9.52'S 144°35.44'E, rubble, SCUBA, 20 m, S. Keable, 25 Jan 1993.
QLD 759 Gutter in reef flat, Boot Reef, Coral Sea, Queensland, 10°2.72'S 144°41.93'E, *Halimeda*, SCUBA, 4 m, S. Keable, 27 Jan 1993.

QLD 760 Reef flat, Boot Reef, Coral Sea, Queensland, 10°2.72'S 144°41.93'E, rubble, SCUBA, 4 m, S. Keable, 27 Jan 1993.

QLD 777 Reef slope, Portlock Reef, Coral Sea, Queensland, 9°38.58'S 144°49.67'E, SCUBA, 30 m, S. Keable, 29 Jan 1993.

QLD 856 Boat Rock, North Stradbroke Island, Queensland, 27°25.21'S 153°33.28'E, olive green massive sponge (*Psammocinia*), collected by hand on SCUBA, 22 m, 21.8°C, G.D.F. Wilson, 3 Jun 1993.

QLD 921 Sabina Point, Shoalwater Bay, Queensland, 22°23.73'S 150°18.15'E, sand, silt and algae in tide pools at low tide, collected with 100 micron hand net, 1 m, 24.0°C, G.D.F. Wilson, 15 Sep 1993.

QLD 949 SW end of Dome Island, Hervey Islands, Queensland, 22°24.78'S 150°44.65'E, algae covered cobbles, collected by airlift, 4 m, 22.6°C, G.D.F. Wilson, 19 Sep 1993.

QLD 954 SW end of Dome Island, Hervey Islands, Queensland, 22°24.78'S 150°44.65'E, *Sargassum*, collected by hand on SCUBA, 6 m, 22.6°C, A. Murray, 19 Sep 1993.

QLD 955 SW end of Dome Island, Hervey Islands, Queensland, 22°24.78'S 150°44.65'E, scrapings from rock, *Halimeda, Dictyota, Lobophora* and *corallines*, collected by hand on SCUBA, 6 m, 22.6°C, A. Murray, 19 Sep 1993.

QLD 957 SE Quoin Island, Port Clinton, Queensland, 22°34.02'S 150°47.89'E, *Caulerpa, Codium* and sponges of rocky ridge, collected by hand on SCUBA, 10 m, 22.4°C, A. Murray, 20 Sep 1993.

QLD 968 Island off S end of Freshwater Bay, Queensland, 22°38.84'S 150°47.52'E, *Sargassum*, collected by hand on snorkel, 2 m, 23.0°C, G.D.F. Wilson, 21 Sep 1993.

QLD 969 Island off S end of Freshwater Bay, Queensland, 22°38.84'S 150°47.52'E, mixed benthic habitat, collected by hand on snorkel, 2 m, 23.0°C, A. Murray, 21 Sep 1993.

QLD 972 Island off S end of Freshwater Bay, Queensland, 22°38.84'S 150°47.52'E, algae ?*Dictyota*, collected by hand on snorkel, 2 m, 23.0°C, G.D.F. Wilson, 21 Sep 1993.

QLD 979 Island off S end of Freshwater Bay, Queensland, 22°38.84'S 150°47.52'E, from underside of boulders, collected by airlift on SCUBA, 3 m, 22.4°C, K.B. Attwood, 22 Sep 1993.

QLD 980 Island off S end of Freshwater Bay, Queensland, 22°38.84'S 150°47.52'E, sponge and ascidian from underneath rock, collected by hand on SCUBA, 3 m, 22.4°C, G.D.F. Wilson, 22 Sep 1993.

QLD 983 Island off S end of Freshwater Bay, Queensland, 22°38.84'S 150°47.52'E, eunicid tubes and ascidians under rock ledge, collected by hand on SCUBA, 3 m, 22.4°C, A. Murray, 22 Sep 1993.

QLD 985 Island off southern end of Freshwater Bay, Queensland, 22°38.84'S 150°47.52'E, piece of wood, collected by hand on SCUBA, 3 m, 22.4°C, G.D.F. Wilson, 22 Sep 1993.

QLD 986 Island off S end of Freshwater Bay, Queensland, 22°38.84'S 150°47.52'E, from worm tubes from underside of ledge, collected by hand on SCUBA, 4 m, 22.4°C, A. Murray, 22 Sep 1993.

QLD 990 Island off S end of Freshwater Bay, Queensland, 22°38.84'S 150°47.52'E, onophid tubes and rubble from bottom, collected by hand on SCUBA, 3 m, 22.4°C, A. Murray, 22 Sep 1993.

Lizard Island (sampling targeted on the Caprellidae).

All samples are preserved in 95% ethanol:

QLD 1464 W side of Blue Lagoon between Palfrey Island and Lizard Island, Queensland, broken *Acropora* heavily encrusted with brown/green filamentous algae, collected by hand on SCUBA, 2–3 m, J.M. Guerra-García & S.J. Keable, 7 Oct 2001.

QLD 1465 W side of Blue Lagoon between Palfrey Island and Lizard Island, Queensland, *Turbinaria ornata*, collected by hand on SCUBA, 2–3 m, J.M. Guerra-García & S.J. Keable, 7 Oct 2001.

QLD 1468 W side of Blue Lagoon between Palfrey Island and Lizard Island, Queensland, colony of small brown tunicate cf. *Aplidium* sp., collected by hand on SCUBA, 2–3 m, J.M. Guerra-García & S.J. Keable, 7 Oct 2001.

QLD 1469 W side of Blue Lagoon between Palfrey Island and Lizard Island, Queensland, coral rubble, collected by hand on SCUBA, 2–3 m, J.M. Guerra-García & S.J. Keable, 7 Oct 2001.

QLD 1470 Blue Lagoon, Lizard Island, Queensland, hydroid *Gymnangium* sp. on hard coral, collected by hand on SCUBA, 9 m, Soren Sehubert, Oct 2001.

QLD 1472 Coconut Beach, Lizard Island, Queensland, hydroid *Aglaophenia cupressina*, collected by hand on SCUBA, 3–4 m, J.M. Guerra-García & S.J. Keable, 8 Oct 2001.

QLD 1473 Coconut Beach, Lizard Island, Queensland, dead *Junceella* (sea whip) heavily encrusted with various epiphytes, collected by hand on SCUBA, 12 m, J.M. Guerra-García & S.J. Keable, 8 Oct 2001.

QLD 1474 Coconut Beach, Lizard Island, Queensland, hydroid *Macrorhynchia philippina*, collected by hand on SCUBA, 4 m, J.M. Guerra-García & S.J. Keable, 8 Oct 2001.

QLD 1475 Coconut Beach, Lizard Island, Queensland, dead thick branching hard coral encrusted with calcareous red algae and filamentous algal turf, collected by hand on SCUBA, 8 m, J.M. Guerra-García & S.J. Keable, 8 Oct 2001.

QLD 1476 Coconut Beach, Lizard Island, Queensland, fine live hard coral encrusted with calcareous red algae and filamentous red/green/brown algal turf, collected by hand on SCUBA, 6 m, J.M. Guerra-García & S.J. Keable, 8 Oct 2001.

QLD 1477 Coconut Beach, Lizard Island, Queensland, coral rubble, branching pieces and flat piece with small holes, collected by hand on SCUBA, 10–13 m, J.M. Guerra-García & S.J. Keable, 8 Oct 2001.

QLD 1478 Coconut Beach, Lizard Island, Queensland, coarse shelly sediment, collected by hand on SCUBA, 12 m, J.M. Guerra-García & S.J. Keable, 8 Oct 2001.

QLD 1482 Crystal Beach, Lizard Island, Queensland, low white encrusting sponge cf. *Dysidea* sp. from underside of cave roof, collected by hand on SCUBA, 7 m, J.M. Guerra-García & S.J. Keable, 9 Oct 2001.

QLD 1483 Crystal Beach, Lizard Island, Queensland, thick branching coral rubble encrusted with red algal turf and black sponge half buried in sediment, collected by hand on SCUBA, 5 m, J.M. Guerra-García & S.J. Keable, 9 Oct 2001.

QLD 1484 Crystal Beach, Lizard Island, Queensland, hydroid *Macrorhynchia philippina*, collected by hand on SCUBA, 3 m, J.M. Guerra-García & S.J. Keable, 9 Oct 2001.

QLD 1485 Crystal Beach, Lizard Island, Queensland, thin branching living coral heavily encrusted with brown/green algal turf and red calcareous algae, collected by hand on SCUBA, 4 m, J.M. Guerra-García & S.J. Keable, 9 Oct 2001.

QLD 1486 Crystal Beach, Lizard Island, Queensland, coarse sediment composed largely of spiny foraminifera with some shell, collected by hand on SCUBA, 9–9.4 m, J.M. Guerra-García & S.J. Keable, 9 Oct 2001.

QLD 1487 Crystal Beach, Lizard Island, Queensland, coarse sediment composed largely of spiny foraminifera with some shell and small pieces of coral rubble, collected by hand on SCUBA, 4–5 m, J.M. Guerra-García & S.J. Keable, 9 Oct 2001.

QLD 1488 Just N of Turtle Beach, Lizard Island, Queensland, branching coral rubble heavily encrusted with calcareous red algae and algal turf, collected by hand on SCUBA, 6 m, J.M. Guerra-García & S.J. Keable, 10 Oct 2001.

QLD 1503 Just N of Turtle Beach, Lizard Island, Queensland, clump of silty algae cf. *Halymenia*, collected by hand on SCUBA, 14 m, J.M. Guerra-García & S.J. Keable, 10 Oct 2001.

QLD 1505 Just N of Turtle Beach, Lizard Island, Queensland, hydroid *Macrorhynchia philippina*, collected by hand on SCUBA, 14 m, J.M. Guerra-García & S.J. Keable, 10 Oct 2001.

QLD 1507 Just N of Turtle Beach, Lizard Island, Queensland, erect brown sponge cf. *Pericharax heteroraphis*, collected by hand on SCUBA, 14 m, J.M. Guerra-García & S.J. Keable, 10 Oct 2001.

QLD 1509 Just N of Turtle Beach, Lizard Island, Queensland, hydroid *Gymnangium* sp. collected by hand on SCUBA, 14 m, J.M. Guerra-García & S.J. Keable, 10 Oct 2001.

QLD 1511 Just N of Turtle Beach, Lizard Island, Queensland, sediment (about 40% <0.5mm remaining 60% shelly and coarse sand), collected by hand on SCUBA, 2–3 m, J.M. Guerra-García & S.J. Keable, 10 Oct 2001.

QLD 1514 Watsons Bay, Lizard Island, Queensland, sediment (c. 65% <0.5 mm, remaining c. 35% coarse (5 mm) shell, *Halimeda* flakes and forams cf. *Marginopora vertebralis*), collected by hand on SCUBA, 18 m, J.M. Guerra-García & S.J. Keable, 11 Oct 2001.

QLD 1515 Watsons Bay, Lizard Island, Queensland, petrified branching stick covered in fine filamentous red algae, calcareous red algae and small brown alga cf. *Zonaria*, collected by hand on SCUBA, 18 m, J.M. Guerra-García & S.J. Keable, 11 Oct 2001.

QLD 1516 Watsons Bay, Lizard Island, Queensland, *Halimeda cylindracea*, collected by hand on SCUBA, 18 m, J.M. Guerra-García & S.J. Keable, 11 Oct 2001.

QLD 1517 Watsons Bay, Lizard Island, Queensland, orange convoluted sponge cf. *Clathria* with some small algae *Udotea*, collected by hand on SCUBA, 18 m, J.M. Guerra-García & S.J. Keable, 11 Oct 2001.

QLD 1519 Watsons Bay, Lizard Island, Queensland, mixed sample of *Caulerpa taxifolia* some *Halimeda* cf. *macroloba* some *Udotea* and some flocculent material, collected by hand on SCUBA, 18 m, J.M. Guerra-García & S.J. Keable, 11 Oct 2001.

QLD 1520 Watsons Bay, Lizard Island, Queensland, *Caulerpa taxifolia*, collected by hand on SCUBA, 18 m, J.M. Guerra-García & S.J. Keable, 11 Oct 2001.

QLD 1522 Watsons Bay, Lizard Island, Queensland, alga cf. *Gracilaria* on dead *Halimeda cylindracea* with sediment (fine sand and shell), collected by hand on SCUBA, 18 m, J.M. Guerra-García & S.J. Keable, 11 Oct 2001.

QLD 1523 Just N of Chinaman's Ridge, Lizard Island, Queensland, sediment (fine sand and shell) next to reef, collected by hand on snorkel, 4 m, J.M. Guerra-García & S.J. Keable, 11 Oct 2001.

QLD 1524 Chinamans Ridge, Lizard Island, Queensland, *Padina* cf. *gymnospora* from reef, collected by hand on snorkel, 2 m, J.M. Guerra-García & S.J. Keable, 11 Oct 2001.

QLD 1525 NW edge of Palfrey Island, Lizard Island, Queensland, hydroid cf. *Macrorhynchia philippina*, collected by hand on SCUBA, 6 m, J.M. Guerra-García & S.J. Keable, 12 Oct 2001.

QLD 1526 NW edge of Palfrey Island, Lizard Island, Queensland, *Halimeda micronesica* and *H. macroloba*, collected by hand on SCUBA, 3 m, J.M. Guerra-García & S.J. Keable, 12 Oct 2001.

QLD 1527 NW edge of Palfrey Island, Lizard Island, Queensland, hydroid *Gymnangium* sp., collected by hand on SCUBA, 6 m, J.M. Guerra-García & S.J. Keable, 12 Oct 2001.

QLD 1528 NW edge of Palfrey Island, Lizard Island, Queensland, dead *Junceella* heavily encrusted with red algal turf and calcareous red algae, collected by hand on SCUBA, 12 m, J.M. Guerra-García & S.J. Keable, 12 Oct 2001.

QLD 1529 NW edge of Palfrey Island, Lizard Island, Queensland, *Padina* sp., collected by hand on SCUBA, 3–12 m, J.M. Guerra-García & S.J. Keable, 12 Oct 2001.

QLD 1531 NW edge of Palfrey Island, Lizard Island, Queensland, dead gorgonian with epiphytes, collected by hand on SCUBA, 12 m, J.M. Guerra-García & S.J. Keable, 12 Oct 2001.

QLD 1532 NW edge of Palfrey Island, Lizard Island, Queensland, sediment (coarse-medium sand with c. 35% medium shell), collected by hand on SCUBA, 12 m, J.M. Guerra-García & S.J. Keable, 12 Oct 2001.

QLD 1533 N end of Mermaid Beach, Lizard Island, Queensland, *Padina* sp., collected by hand on snorkel, 4 m, J.M. Guerra-García & S.J. Keable, 12 Oct 2001.

QLD 1536 Blue Lagoon between Bird Islet and South Island, Lizard Island, Queensland, mixed encrusted coral rubble, collected by hand on SCUBA, 2 m, J.M. Guerra-García & S.J. Keable, 13 Oct 2001.

QLD 1537 Blue Lagoon between Bird Islet and South Island, Lizard Island, Queensland, fine sediment (100% <0.5 mm), collected by hand on SCUBA, 10 m, J.M. Guerra-García & S.J. Keable, 13 Oct 2001.

QLD 1538 Blue Lagoon between Bird Islet and South Island, Lizard Island, Queensland, sediment (medium grained sand), collected by hand on SCUBA, 6 m, J.M. Guerra-García & S.J. Keable, 13 Oct 2001.

QLD 1541 Reef slope on S side of South Island, Lizard Island, Queensland, gorgonian cf. *Paracis* sp., collected by hand on SCUBA, 20 m, J.M. Guerra-García & S.J. Keable, 14 Oct 2001.

QLD 1543 Reef slope on S side of South Island, Lizard Island, Queensland, unidentified fine delicate hydroid, collected by hand on SCUBA, 25 m, J.M. Guerra-García & S.J. Keable, 14 Oct 2001.

QLD 1544 Reef slope on S side of South Island, Lizard Island, Queensland, gorgonian cf. *Menella* sp., collected by hand on SCUBA, 25 m, J.M. Guerra-García & S.J. Keable, 14 Oct 2001.

QLD 1545 Reef slope on S side of South Island, Lizard Island, Queensland, gorgonian cf. *Mopsella* sp., collected by hand on SCUBA, 20 m, J.M. Guerra-García & S.J. Keable, 14 Oct 2001.

QLD 1546 Reef slope on S side of South Island, Lizard Island, Queensland, hydroid *Aglaophenia delicatula*, collected by hand on SCUBA, 20 m, J.M. Guerra-García & S.J. Keable, 14 Oct 2001.

QLD 1547 Reef slope on S side of South Island, Lizard Island, Queensland, hydroid *Macrorhynchia philippina*, collected by hand on SCUBA, 10–20 m, J.M. Guerra-García & S.J. Keable, 14 Oct 2001.

QLD 1549 Reef slope on S side of South Island, Lizard Island, Queensland, coarse coral sediment with some small gravel and rubble, collected by hand on SCUBA, 20 m, J.M. Guerra-García & S.J. Keable, 14 Oct 2001.

QLD 1550 Reef slope on S side of South Island, Lizard Island, Queensland, purple tube sponge cf. *Kallypilidion* sp., collected by hand on SCUBA, 20 m, J.M. Guerra-García & S.J. Keable, 14 Oct 2001.

QLD 1553 North Point, Lizard Island, Queensland, hydroid cf. *Aglaophenia* sp. (not *A. cupressina*), collected by hand on SCUBA, 7 m, J.M. Guerra-García & S.J. Keable, 14 Oct 2001.

QLD 1554 North Point, Lizard Island, Queensland, mixed hydroids (*Aglaophenia, Gymnangium* and *Macrorhynchia*) from walls and caves of canyon with strong current, collected by hand on SCUBA, 5–6 m, J.M. Guerra-García & S.J. Keable, 14 Oct 2001.

QLD 1557 Outer reef slope midway between Bird Islet and South Island, Lizard Island, Queensland, caprellids from small orange gorgonian, collected by hand on SCUBA, 6 m, J.M. Guerra-García & S.J. Keable, 15 Oct 2001.

QLD 1559 Outer reef slope midway between Bird Islet and South Island, Lizard Island, Queensland, tunicates cf. *Polycarpa pigmentata* encrusted with algal turf and hydroids from sediment slope, collected by hand on SCUBA, 20 m, J.M. Guerra-García & S.J. Keable, 15 Oct 2001.

QLD 1560 Outer reef slope midway between Bird Islet and South Island, Lizard Island, Queensland, hydroid *Salacia* n.sp. from sediment slope, collected by hand on SCUBA, 25 m, J.M. Guerra-García & S.J. Keable, 15 Oct 2001.

QLD 1561 Outer reef slope midway between Bird Islet and South Island, Lizard Island, Queensland, hydroid *Macrorhynchia phoenicia* from sediment slope, collected by hand on SCUBA, 10–15 m, J.M. Guerra-García & S.J. Keable, 15 Oct 2001.

QLD 1562 Outer reef slope midway between Bird Islet and South Island, Lizard Island, Queensland, hydroid *Macrorhynchia philippina* from sediment slope, collected by hand on SCUBA, c. 10 m, J.M. Guerra-García & S.J. Keable, 15 Oct 2001.

QLD 1563 Outer reef slope midway between Bird Islet and South Island, Lizard Island, Queensland, coarse shelly sediment from slope with some foraminifera (cf. *Marginopora*) and *Halophila ovalis*, collected by hand on SCUBA, 15–20 m, J.M. Guerra-García & S.J. Keable, 15 Oct 2001.

QLD 1564 Reef slope S of "Washing Machine", NE side of Lizard Island, Queensland, mixed hydroids (90% brown unidentified species, remainder *Macrorhynchia philippina*), collected by hand on SCUBA, 5 m, J.M. Guerra-García & S.J. Keable, 16 Oct 2001.

QLD 1565 Reef slope S of "Washing Machine", NE side of Lizard Island, Queensland, caprellids from brown sponge cf. *Clathria reinwardti*, collected by hand on SCUBA, 18 m, J.M. Guerra-García & S.J. Keable, 16 Oct 2001.

QLD 1567 Reef slope S of "Washing Machine", NE side of Lizard Island, Queensland, hydroid cf. *Solanderia* sp. from cave, collected by hand on SCUBA, 6 m, J.M. Guerra-García & S.J. Keable, 16 Oct 2001.

QLD 1568 Reef slope S of "Washing Machine", NE side of Lizard Island, Queensland, *Halimeda macroloba*, collected by hand on SCUBA, 6 m, J.M. Guerra-García & S.J. Keable, 16 Oct 2001.

QLD 1569 Reef slope S of "Washing Machine", NE side of Lizard Island, Queensland, sediment with *Halimeda cylindracea*, some *Udotea* and *Caulerpa* sp., collected by hand on SCUBA, 5 m, J.M. Guerra-García & S.J. Keable, 16 Oct 2001.

QLD 1570 Reef slope S of "Washing Machine", NE side of Lizard Island, Queensland, mixed hydroids (*Aglaophenia* sp., *Gymnangium gracilicaule, Macrorhynchia philippina* and large unidentified species), collected by hand on SCUBA, 3 m, J.M. Guerra-García & S.J. Keable, 16 Oct 2001.

QLD 1571 Reef slope S of "Washing Machine", NE side of Lizard Island, Queensland, large brown sponge cf. *Jaspis* sp., collected by hand on SCUBA, 15–20 m, J.M. Guerra-García & S.J. Keable, 16 Oct 2001.

QLD 1572 Reef slope S of "Washing Machine", NE side of Lizard Island, Queensland, fine sand with small amount of fine shell, collected by hand on SCUBA, 20–25 m, J.M. Guerra-García & S.J. Keable, 16 Oct 2001.

QLD 1573 Reef slope S of "Washing Machine", NE side of Lizard Island, Queensland, mixed silty filamentous red algae (not yet collected at previous stations) a little *Caulerpa taxifolia*, collected by hand on SCUBA, 6 m, J.M. Guerra-García & S.J. Keable, 16 Oct 2001.

QLD 1574 Off front of patch reefs at N end of Casuarina Beach, Lizard Island, Queensland, medium grained sand, collected by hand on snorkel, 4 m, J.M. Guerra-García & S.J. Keable, 16 Oct 2001.

QLD 1575 No Name Reef, Dynamite Passage outer Great Barrier Reef east of Lizard Island, Queensland, medium-fine grained sand with some silt, collected by hand on SCUBA, 10 m, J.M. Guerra-García & S.J. Keable, 17 Oct 2001.

QLD 1576 No Name Reef, Dynamite Passage outer Great Barrier Reef east of Lizard Island, Queensland, hydroid *Macrorhynchia philippina*, collected by hand on SCUBA, 10 m, J.M. Guerra-García & S.J. Keable, 17 Oct 2001.

QLD 1578 Pidgin Point, Lizard Island, Queensland, compact globular tan coloured sponge cf. *Xentospongia* sp. with some algal turf covering (fiborous when cut) from under coral ledge, collected by hand on SCUBA, 20 m, J.M. Guerra-García & S.J. Keable, 18 Oct 2001.

QLD 1579 Pidgin Point, Lizard Island, Queensland, hydroid *Macrorhynchia philippina* near sediment, collected by hand on SCUBA, 20–25 m, J.M. Guerra-García & S.J. Keable, 18 Oct 2001.

QLD 1580 Pidgin Point, Lizard Island, Queensland, hydroid *Halopteris buskii*., collected by hand on SCUBA, 5–10 m, J.M. Guerra-García & S.J. Keable, 18 Oct 2001.

QLD 1581 Pidgin Point, Lizard Island, Queensland, sponge cf. *Clathria reinwardti*, collected by hand on SCUBA, 20 m, J.M. Guerra-García & S.J. Keable, 18 Oct 2001.

QLD 1582 Pidgin Point, Lizard Island, Queensland, fine-medium sand with small amount of shell and coral gravel, collected by hand on SCUBA, 26 m, J.M. Guerra-García & S.J. Keable, 18 Oct 2001.

QLD 1585 Reef just SW of Osprey Island, Lizard Island, Queensland, large amount of hydroid *Macrorhynchia philippina*, collected by hand on SCUBA, 5–10 m, J.M. Guerra-García & S.J. Keable, 18 Oct 2001.

QLD 1588 Reef just SW of Osprey Island, Lizard Island, Queensland, fine-medium sand with some shell, collected by hand on SCUBA, 10–12 m, J.M. Guerra-García & S.J. Keable, 18 Oct 2001.

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